

## REVISION, PHYLOGENY AND BIOGEOGRAPHIC COMMENTS ON THE CIRCUMTROPICAL MARINE PERCOID FISH FAMILY PRIACANTHIDAE

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### ABSTRACT

The circumtropically distributed marine percoid family Priacanthidae, the bigeyes, is a relatively small (18 species in four genera) group of epibenthic predatory fishes occurring primarily in rocky or coral habitats at depths from 5 to 400 m or more. Two species are circumtropical in distribution, 13 occur in portions of the Indo-Pacific, one is confined to the eastern Pacific and two to the Atlantic. Complete familial, generic and species diagnoses and descriptions are given including osteology and scale morphology and complex nomenclatural problems are addressed. Five species in the genus *Priacanthus* are described as new and additional, taxonomically more cryptic, undescribed forms may exist pending acquisition of critical material. Hermaphroditism may occur in some individuals. Priacanthids possess several remarkable features including extremely modified scales, swimbladder modifications, extrinsic swimbladder muscles, unique eye morphology, and osteological conditions which were useful in hypothesizing relationships and corroborating the monophyly of the family. The genus *Pristigenys* (4 species) is hypothesized to be the sister group to all other priacanthids; *Cookeolus* (monotypic) is the sister group to *Heteropriacanthus* (monotypic) plus *Priacanthus* (12 species). Intrageneric relationships are hypothesized. No hypothesis of the phylogenetic position of priacanthids among percoids could be advanced. Correlation of the hypothesized familial phylogeny and the fossil record suggests that evolution of all genera predated the Miocene. Species level relationships indicate a closer relationship among species of the Hawaiian Islands and species to the southeast or east (Easter I., eastern Pacific, Atlantic) than either of these areas has to the west Pacific. Possible vicariant biogeographic scenarios are discussed along with problems of advancing biogeographic hypotheses for species groups having distributions interrupted by vast regions.

Priacanthids, commonly called the bigeyes, comprise a relatively small circumtropical family (18 species currently known) of marine percoid fishes. They reach maximum diversity in the Indo-Pacific region with one species confined to the eastern Pacific and two to the Atlantic Ocean. The family's members are characterized generally by extremely large eyes, deep bodies, rough scales, and primarily bright red life coloration. Priacanthids are especially noted for their remarkable "eyeshine"; the brilliant reflective layer of their large eyes, or tapida lucidum, may be of a unique type among teleosts. The extreme roughness of their scales, which are not ctenoid but bear integral spines, results from several apparently unique modifications. Adults of most species typically average less than 30 cm total length, although the largest attains lengths in excess of 50 cm. External sexual dimorphism is not evident, except possibly in one species, and at least one species may occasionally exhibit hermaphroditism. Twelve species possess extrinsic swimbladder muscles to aid in sound production.

Bigeye are epibenthic in habit and are generally associated with rock formations or coral reefs where they lurk in or near crevices or beneath ledges through at least most of the daytime hours; however a few species are often trawled in more open bottom areas. They occur from depths of less than 5 to perhaps 400 or more m. Species of priacanthids are known to feed primarily on crustaceans, small cephalopods, polychaetes, and small fishes. They are believed to be most active nocturnally but some species are known to also feed diurnally, at least in cave

habitats. Eggs, larvae and early juvenile stages are pelagic, transforming upon settling in suitable habitat.

Priacanthids are tropical and subtropical in distribution, extending into temperate regions in association with warm ocean currents, but are notably absent from the subtropical or warm-temperate faunas of northern New Zealand and the Mediterranean region. Some species are very important in the trawl fisheries of southeast Asia but the group is of generally lesser economic importance in other regions, being taken only incidentally in trawls and by hook and line. Some of the general vernacular names for these fishes are "bigeye," "bulleye," "glasseye snapper" (America), "catalufa" (many Spanish-speaking countries), "olho-de-cão" (Brazil, Madeira), "scad" and "goggle-eye" (S. Africa), "bullseye" (Australia), "pasuwa" and "kewai" (India), "aweoweo" (Hawaii), "maere" (French Polynesia), "pla-ta-to" (Thailand), and "kintoki" (Japan).

The family Priacanthidae was first erected by Gill (1872) based on the percoid group "Priacanthina" of Günther (1859), which treated all species as members of the genus *Priacanthus* Oken. *Pristigenys* Agassiz (1835) was not included in the family until a century after its description (White, 1936). Boulenger (1895) classified the group as a subfamily of Serranidae, in which he also included present-day centropomids. The group has been treated at the familial level in all subsequent classifications. The phylogenetic position of Priacanthidae with respect to all other families placed in the provisional, and perhaps unnatural, perciform suborder Percoidei, as well as families currently ascribed to Beryciformes, is unclear, a situation comparable to the majority of families in those groups (Lauder and Leim, 1983; Johnson, 1984).

There has been considerable taxonomic confusion among priacanthid species. At the generic level, the early nomenclatural history of *Priacanthus* is a bit convoluted, that of *Pristigenys* has been controversial, and nomenclature of the types of the remaining two genera has been problematic.

Aside from numerous brief treatments in various general classifications and regional faunal works, literature dealing specifically with the Priacanthidae as a group began with that of Bleeker (1873a) who treated species of the Indonesian region. Morrison (1889) reviewed the American species, Caldwell (1962a) those of the western Atlantic. Myers (1958) and Smith (1966) compared members of the genus *Pristigenys* and gave distributional information. Eggleston (1974) presented accounts of the western Pacific-eastern Indian Ocean species, Randall (1978) those of the western Atlantic, and Starnes (1981, 1984) those of the eastern Atlantic and western Indian Ocean respectively. Lee (1980) reviewed the Priacanthidae of Taiwan and later (1984) published biochemical systematic studies of these fishes. Fitch and Crooke (1984) treated eastern Pacific priacanthids and described a new genus, *Heteropriacanthus*, for one species. Shao and Chang (1985) advanced a hypothesis of the phylogenetic relationships of the species of Taiwan based on morphometric analyses. A catalog of the many priacanthid types present in the Museum National D'Histoire Naturelle in Paris is being completed by M. L. Bauchot. In addition, Salmon and Winn (1966) analyzed sound production in two Hawaiian species and Senta (1977, 1978) reported on fisheries biology aspects of several species in southeast Asian waters.

Prior to this study, no comprehensive systematic analysis of the Recent Priacanthidae has been attempted on a worldwide basis, nor have extensive comparative anatomical studies been conducted as a basis for hypotheses of intrafamilial, and possibly extrafamilial, relationships. As construed herein, the family consists of 18 species in four genera, two of which are monotypic. Four species in the genus *Priacanthus* are described as new, including one in collaboration with J. T.

Moyer who independently recognized it as distinct. An additional undescribed form may occur in the Galapagos Islands and some specimens treated here as *P. macracanthus* may be representative of polytypy. Resolution of these questions requires acquisition of further critical materials. Despite relatively extensive anatomical comparisons with other perciform and beryciform groups, no hypothesis of the extrafamilial relationships of Priacanthidae resulted from this study.

In addition to Recent species, several fossil teleosts, from the Eocene, Oligocene and Miocene of Europe and the Middle East, have been provisionally ascribed to the family Priacanthidae; all are placed in the genera *Priacanthus* and *Pristigenys*. Fitch and Crooke (1984) have most recently discussed the status of those ascribed to *Pristigenys*. The status of all fossil species and their possible relationships to Recent species will be the subject of a later study.

#### METHODS AND MATERIALS

Counts and measurements are as prescribed by Hubbs and Lagler (1958) except body depth was measured from homologous landmarks (fourth dorsal spine in *Pristigenys*, sixth in other genera). These landmarks are approximately above the maximum body depth points for these groups but are not necessarily extremal for all specimens. In addition to standard measurements, truss measurements were conducted on some species for morphometric analyses as outlined in Bookstein et al. (1985). Scales in a lateral series (LS) were counted forward along the lateral-line to its upward deflection on the peduncle, thence anteriorly to the degree possible in a straight line to the supracleithrum. Where scale irregularities were encountered, the count was continued along the upper of the two rows in question. Vertical scale rows (VSR) were counted from the dorsal-fin origin diagonally to the anus. Lateral-line scale counts include all pored scales on the caudal fin base.

Additional abbreviations used are SL (standard length), TL (total length), BD (body depth), BW (body width), CPL (caudal peduncle length), CPD (caudal peduncle depth), HL (head length), HD (head depth), HW (head width), ORB (horizontal bony orbit length), IO (bony interorbital width), SNT (snout length), JW (length of lower jaw or mandible), D1L (length of longest dorsal spine), D2L (length of longest soft dorsal ray), AL (length of longest soft anal ray), P1L (pectoral fin length), P2L (pelvic fin length).

In species accounts, scale and gill raker counts and measurements are given as ranges with means in parentheses; fin ray counts are modal with ranges in parentheses. Measurements are expressed as thousandths of standard length. Assessments of allometry are with respect to standard length. Synonymies are based on examination of types unless otherwise noted in "Remarks" of species accounts.

Myological terminology is that of Winterbottom (1974). Osteological studies were performed primarily on specimens cleared and counterstained for bone and cartilage (method modified from Dingerkus and Uhler, 1977) supplemented by radiographs. Studies of scale morphology were aided by use of scanning electron microscopy.

Univariate and multivariate statistical analyses were performed using the SYSTAT microcomputer package (SYSTAT, Inc.). Phylogenetic methodology follows the tenets for cladistics set forth by Hennig (1965) as refined by various authors (see Wiley, 1981 for review), with relationships hypothesized based on characters estimated to be shared derived. Ideally, in a cladistic analysis characters are polarized with regard to derivedness according to conditions present in hypothesized sister groups (i.e., immediate outgroups). Since few such relationships have been proposed among percoids, and none were elucidated in this study for priacanthids, it was necessary to use a generalized outgroup approach to estimate character polarity. This makes the assumption that prevalent conditions among outgroup members are primitive. For this study, this outgroup consisted of one to several generic representatives of 27 families presently classified (Nelson, 1984) in Perciformes, plus five beryciform families. Where pertinent, these families are noted in the Phylogenetic Analysis. In certain intrageneric analyses, where extrafamilial outgroup comparison was impractical, characters were polarized according to conditions present in sister genera whose relationships were already established by outgroup comparison. These sister genera thus serve as a functional outgroup (Watrous and Wheeler, 1981). Initial cladistic analyses were later corroborated by an analysis employing the global branch-swapping option of the Phylogenetic Analysis Using Parsimony (PAUP) package of D. L. Swofford.

In "Material Examined" sections, "C&S" denotes cleared and stained specimens; "skel" denotes dried skeletons. Specimens were examined from the following institutions with abbreviations in parentheses: American Museum of Natural History, New York (AMNH); Australian Museum, Sydney (AMS); Academy of Natural Sciences of Philadelphia (ANSP); Bernice P. Bishop Museum, Honolulu (BPBM); British Museum (Natural History), London (BMNH); California Academy of Sciences, San Francisco (CAS and SU); Commonwealth Science & Industrial Organization, Hobart, Tasmania (CSI-

RO); Field Museum of Natural History, Chicago (FMNH); Fisheries Research Laboratory, Mie University, Japan (FRLM); Hebrew University, Jerusalem (HUJ); Kanudi Fisheries Research Station, Konedobu, Papua New Guinea (KFRS); Los Angeles County Museum Natural History, Los Angeles (LACM); Museum of Comparative Zoology, Harvard University, Cambridge (MCZ); Museum National d'Histoire Naturelle, Paris (MNHN); Museo Civico di Storia Naturale, Verona, Italy (MSNVR); Museu de Zoologia, Universidade de Sao Paulo, Sao Paulo (MZUSP); National Science Museum, Tokyo (NSMT); Northern Territory Museum, Darwin (NTM); Queensland Museum, Brisbane (QM); Rijksmuseum van Natuurlijke Historie, Leiden (RMNH); Royal Ontario Museum, Toronto (ROM); J. L. B. Smith Institute of Ichthyology, Grahamstown, South Africa (RUSI); Smithsonian Oceanographic Sorting Center, Washington, D.C. (SOSC); Tanaka Memorial Biological Laboratory, Miyakejima, Japan (TMBS); Florida State Museum, Gainesville (UF); University of the Ryukyus, Okinawa (URM); Vanderbilt Marine Museum, Long Island, New York (VMM); University of Miami, Miami (UMML); University of Michigan Museum of Zoology, Ann Arbor (UMMZ); National Museum of Natural History, Washington, D.C. (USNM); Western Australian Museum, Perth (WAM); Zoologisch Museum, Amsterdam (ZMA); Museum für Naturkunde, Universität Humboldt, Berlin (ZMB); Zoologisk Museum, University of Copenhagen (ZMUC).

#### FAMILY PRIACANTHIDAE

*Diagnosis.*—A primarily tropical to subtropical group of epibenthic predatory fishes having deep, laterally compressed, oval to moderately elongate bodies. Attaining total lengths in adults of 200–525 mm. Eyes extremely large. Color predominately reddish. Modified spinous cycloid (not ctenoid) scales covering entire body and head. Fin rays with tiny spinules, dorsal fin continuous with 10 spines and 11–15 soft rays, anal fin with 3 spines and 10–16 soft rays, pectoral-fin rays 17–21. Vertebrae 23 including ural complex. Presently classified within the provisional order Perciformes, suborder Percoidei (Nelson, 1984), and having the following combination of “perciform” characters: pelvic-fin rays I,5; pelvic girdle anterior to pectoral girdle; orbitosphenoid bone lacking; number of principal caudal rays restricted (16). Further defined by the following characters hypothesized to be uniquely derived (see Phylogenetic Analysis): low vertebral and caudal-ray counts (above), highly modified scales, form of first epibranchial, spine at posteroventral angle of preoperculum, spines on infraorbital bones, spinules on fin rays, scales on branchiostegals, adnate pelvic fins, unique morphology of tapida lucidum, and reduction or loss of intercalar bones, postcleithrum, and predorsal bones.

*Description.*—Entire body and most of head covered by thick, extremely adherent, spinous scales which do not bear spines on separate platelets (therefore not ctenoid); scale morphology, size, and number variable within species. Body scales large to small, 38–115 in lateral series. Scales of entire head region, nape and prepectoral area very small and irregularly arranged; scales of lateral surfaces of body below lateral line, belly and prepelvic area arranged roughly in rows, increasing slightly in size posteriorly. Anterior half of body with more scale rows than posterior, resulting in irregularities in alignment of lateral rows. Scales above lateral line more or less parallel with those below. Scales considerably modified in head region (Fig. 1), being concave with reduced numbers (<10) of very stout spinules. Scales of chin most modified and oriented in some cases almost perpendicular to dermis. Scales modified to varied degrees on mandibular, gular, ethmoid-interorbital and supraorbital regions. Less modified scales (flatter, 15–20 spinules) on maxilla, cheek, preopercle and opercle; posterior of preopercle with or without scales. Branchiostegal rays with modified scales. Body with scales more flattened; spine-bearing posterior (apical) field slightly flexed outward with no underlying structure (Fig. 2a–d) to considerably elevated with an underlying prominence or flange (Figs. 2e–h, 3a–h). Spinules on scales variable in number (about 10 to 80 or more) and distribution among species and variable within



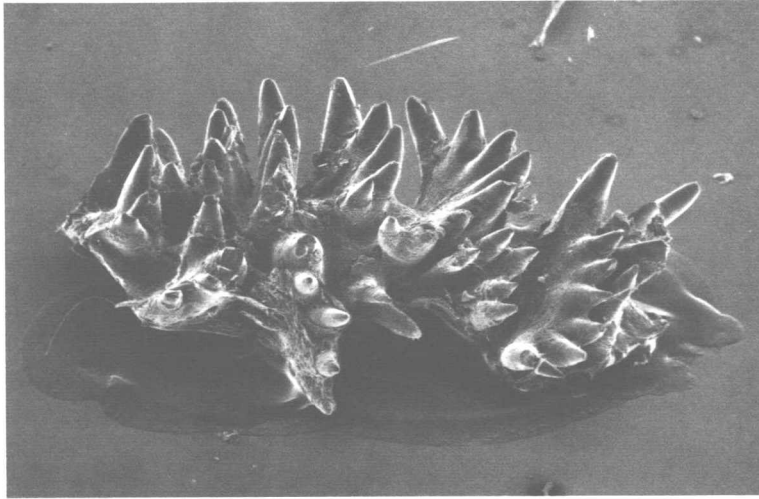


Figure 1. Mandibular scales of *Pristigenys alta*.

individuals with respect to position of scale on body. Anterior field of scales straight-margined or with prominent interradiat projections. Scales covering basal one-fifth of caudal fin; pectoral fin with scales to base of, but not on, rays; pelvic fins with scales basally on ventral surface of rays. Circuli of scales with microscopic denticles ("lepidonts" of Hollander, 1986), corrugations or nearly smooth (Fig. 4a-d). Lateral line highly arched anteriorly, complete onto base of caudal fin, except occasionally for last 2-3 scales; 30-93 pored scales. Lateral-line scales bearing simple tube; scales larger than more ventrally located midlateral scale series, and totaling fewer than horizontal series of the latter.

All fin spines striate. Dorsal-fin rays X (rarely IX or XI), 11-15. Continuous dorsal fin with spinous portion rounded (central spines longest), or graduated with fin lengths increasing posteriorly. Soft portions of dorsal and anal fins rounded or pointed. Anal-fin rays III, 10-16. Caudal fin rounded, truncate, crescentic or lunate, length possibly sexually dimorphic in at least one species, principal rays 8+8. Pectoral fin relatively short and broadly pointed, 17-21 rays. Pelvic fin short to very long, rays I,5, inserted beneath or anterior to pectorals, adnate, attached to belly by a broad membrane along and beyond entire length of medial ray. Anterior three to five dorsal spines with variously developed spinules on anterior surfaces (lost or reduced in adults of some species). Biserial rows of spinules strongly to weakly developed on lateral surfaces of soft dorsal and anal rays. Pectoral rays with uniserial rows of spinules present or absent on lateral surfaces. Basal two-thirds of pelvic-fin rays with spinules variously developed on ventral surface; pelvic spines with spinules developed or absent. Axillary process lacking.

Body moderately deep to very deep, laterally compressed (depth 29-63% of SL). Eye large, diameter about one-half length of head. Mouth strongly oblique, of moderate size. Premaxilla slightly protrusible. Maxilla broad posteriorly and relatively exposed. Lower jaw upturned, strongly projecting. Dentary, premaxilla, vomer and palatine with numerous, small conical teeth, not in rows. Nostrils paired, the anterior rounded, the posterior a transverse slit. Preopercle with serrate margin; a serrate to smooth shelf overlying sensory canal of preopercle with elongate openings of varied length posteriorly; serrate preopercular spine at pos-

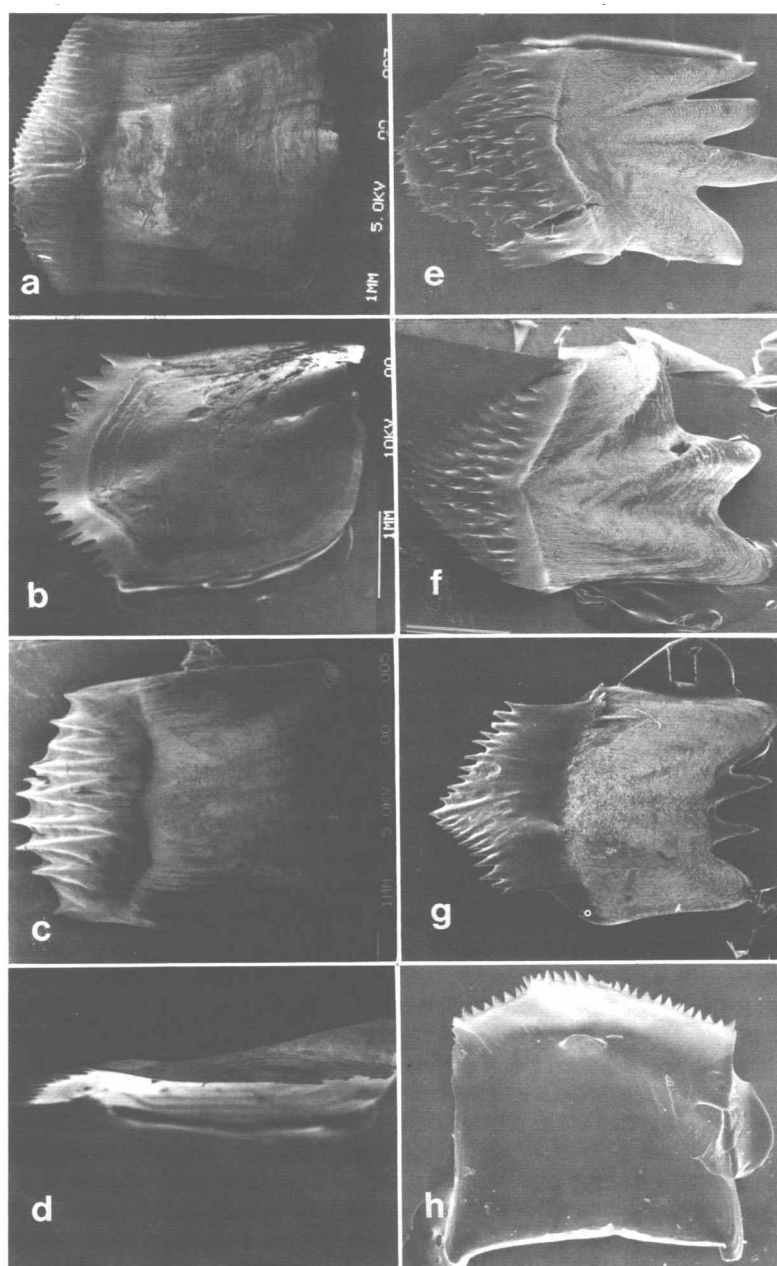


Figure 2. Midlateral scales of priacanthids: a) *Pristigenys niphonia*, 190 mm SL; b) *Pristigenys serrula*, 180 mm SL; c) *Pristigenys meyeri*, 225 mm SL; d) *Pristigenys serrula*, 180 mm SL (edge view); e) *Priacanthus blochii*, 180 mm SL; f) *Priacanthus meeki*, 250 mm SL; g) *Heteropriacanthus cruentatus*, 191 mm SL; h) *Cookeolus japonicus*, 148 mm SL (medial aspect).

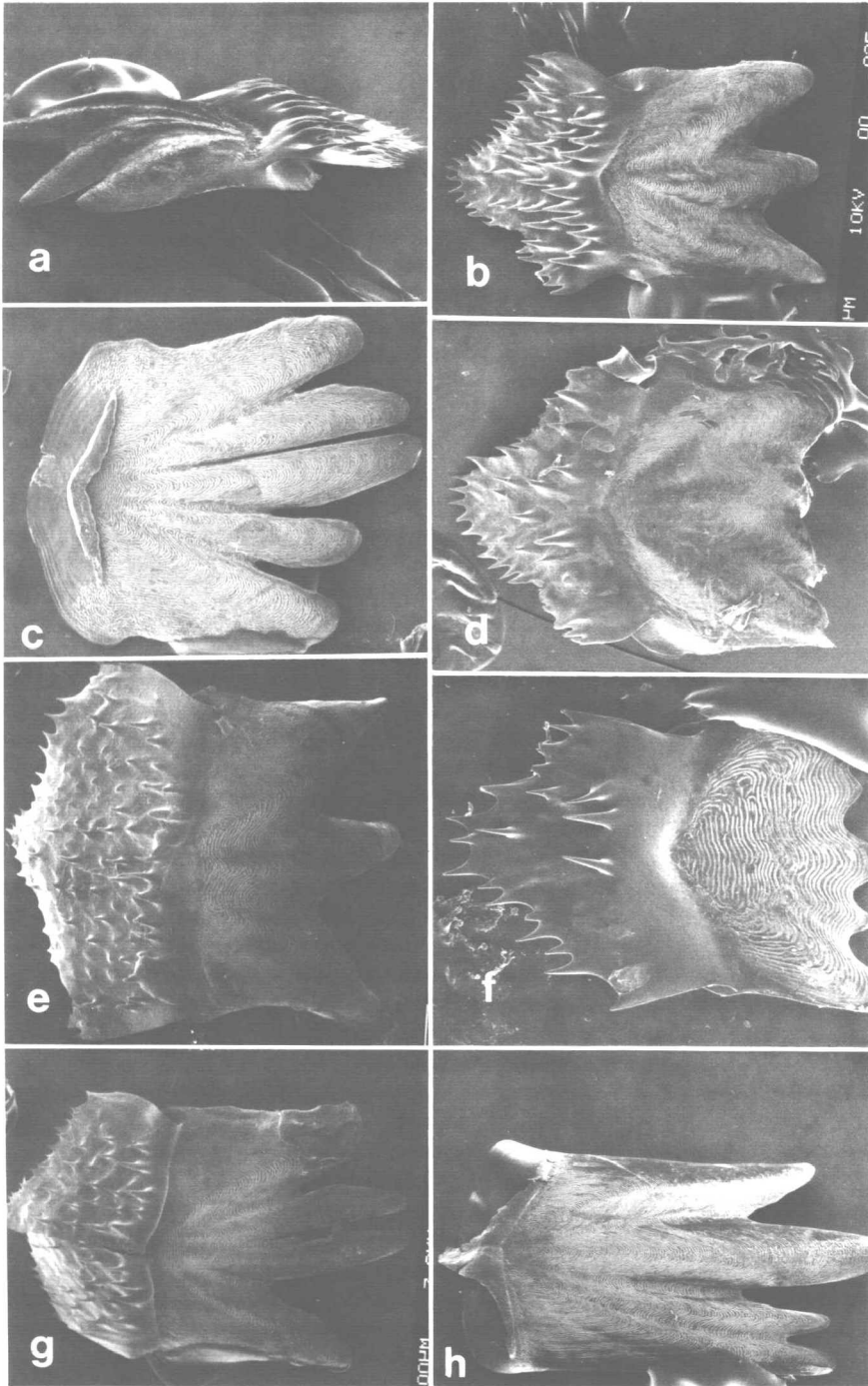


Figure 3. Midlateral scales of *Priacanthus*: a, b) *P. alalaua*, 162 mm SL; c) *P. tayenus*, 168 mm SL; d) *P. zaiserae*, 171 mm SL; e) *P. fuchi*, 185 mm SL; f) *P. sagittarius*, 79 mm SL; g) *P. macracanthus*, 171 mm SL; h) *P. sagittarius*, 202 mm SL.

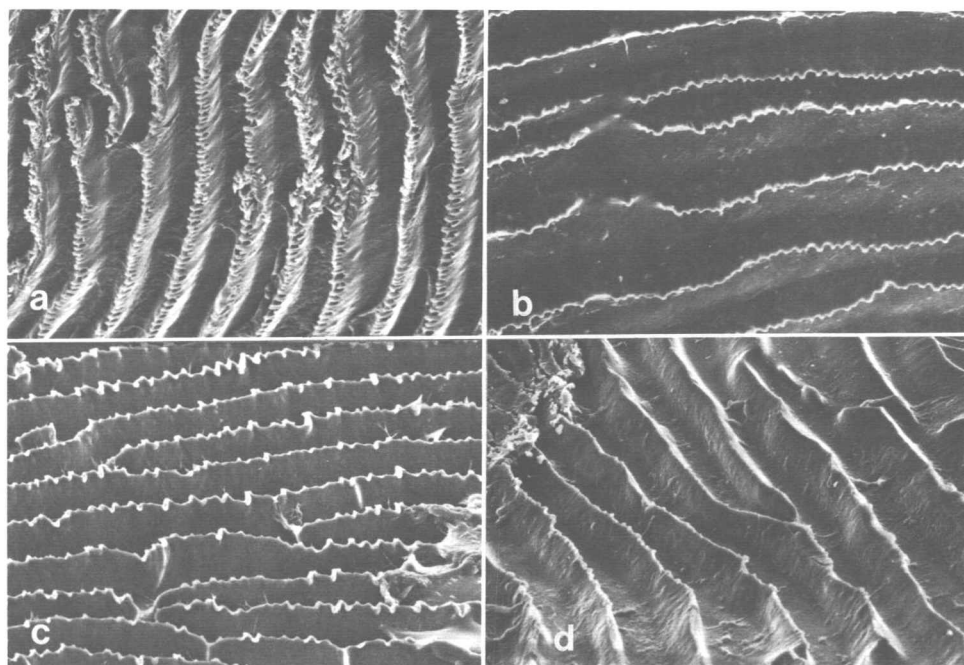


Figure 4. Scanning electron microscope views (about 1,000 $\times$ ) of circuli on midlateral scales of priacanthids: a) *Pristigenys alta*, b) *Cookeolus japonicus*, c) *Heteropriacanthus cruentatus*, d) *Priacanthus hamrur*.

teroverventral angle variously developed. Interopercle elongate, serrate ventrally, pointed anteriorly, broadly pointed to truncate posteriorly or with a deep notch. Opercle relatively narrow with two broad, flat spines, the upper rounded and scarcely protruding. Subopercle asymmetrically V-shaped, ventrally expanded and rounded with serrations. Exposed portions of posttemporal and supracleithrum with serrations. Gill membranes separate, free of isthmus; pseudobranchs well developed, with about 50–75 filaments.

Nasal bones narrow anteriorly, expanded posteriorly, spade-shaped or obliquely truncate; serrations present or absent on margins. Six infraorbitals, finely serrate on inner rim of orbit; lacrymal and second infraorbital of moderate width with spines or fine serrations (Fig. 5a); third to sixth infraorbitals narrow with serrations present or absent ventrally; third infraorbital with a broad subocular shelf. Sensory canal open laterally at joints, on posterior half of lacrymal and ventrolaterally near center of third infraorbital. Two separate supratemporal bones, the anterior a straight, mostly closed to nearly open canal, the second with three short arms bearing canals associated with (but not articulating with) pterotic ventrally and posttemporal posteriorly. Parietal without a medially directed portion of supratemporal canal. Posttemporal scythe-shaped, articulating dorsally at epiotic spine and ventrally with pterotic on medial aspect of its posterior process.

Form of branchial skeleton essentially invariant among genera. First to third basibranchials ossified; fifth ceratobranchials bearing numerous teeth, not fused medially. Pharyngobranchial of first arch elongate, articulating with prootic; second to fourth pharyngobranchials comprise tooth-bearing complex, not fused to one another. Teeth lacking on epibranchials. First epibranchial (Fig. 5b) shaped

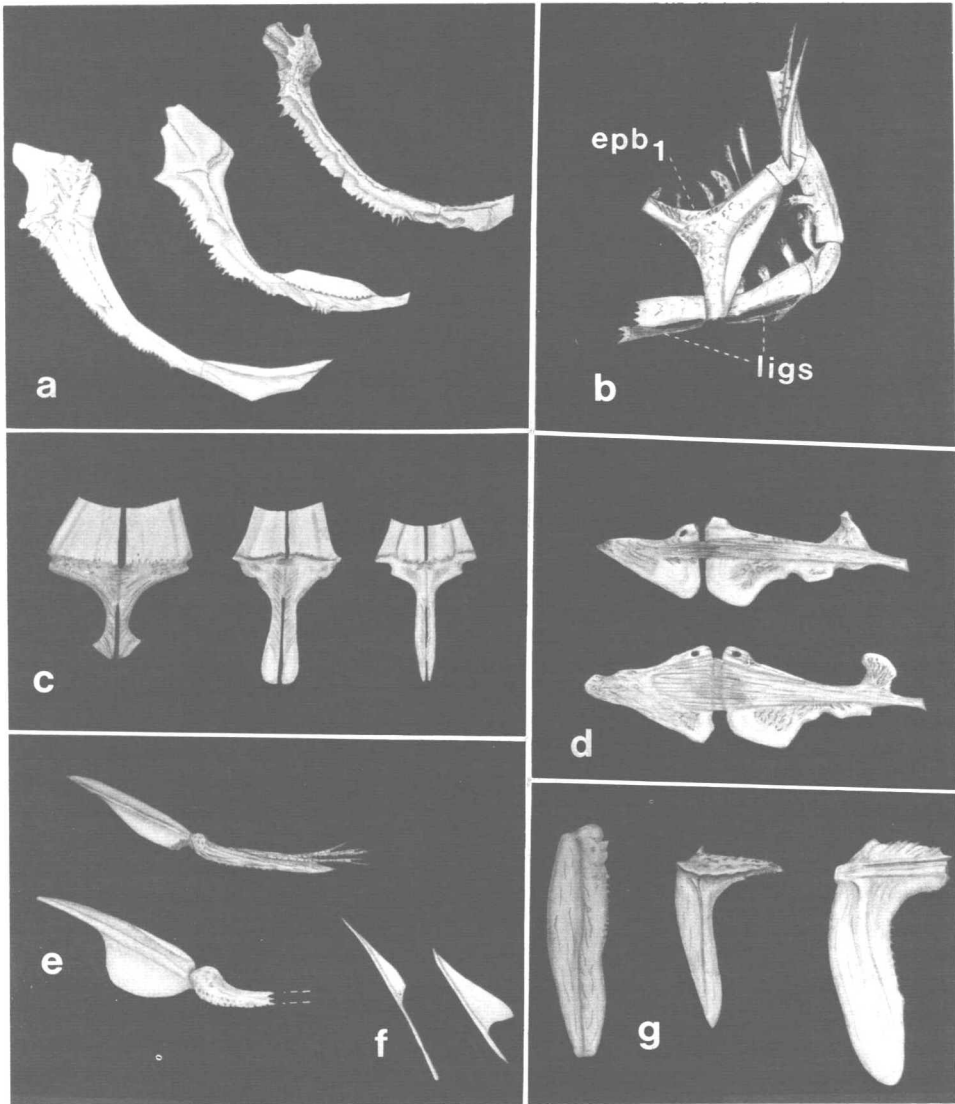


Figure 5. a) left anterior infraorbital bones of (l to r) *Priacanthus sagittarius*, *Priacanthus tayenus*, *Pristigenys alta*; b) right first epibranchial (epb<sub>1</sub>) and ligaments (ligs) and adjacent bones of *Priacanthus sagittarius*; c) postpelvic processes of (l to r) *Pristigenys alta*, *Heteropriacanthus cruentatus*, *Priacanthus sagittarius*; d) left ceratohyal bones of (top) *Pristigenys alta*, (bottom) *Priacanthus sagittarius*; e) pelvic bones (left lat. view) of (top) *Pristigenys alta*, (bottom) *Cookeolus japonicus*; f) pleural ribs associated with ninth vertebra of (l to r) *Priacanthus sagittarius*, *Heteropriacanthus cruentatus*; g) supracleithra of (l to r) *Priacanthus sagittarius*, *Cookeolus japonicus* at 38 mm SL and same at 148 mm SL.

as a flanged-T or broad "Y," the posterior process bearing ligamentous attachments to basal flange of epibranchial 2 and to vicinity of joint of that bone and its associated pharyngobranchial. Interarcual cartilage lacking. Gill rakers slender and relatively elongate, 17–32 on first arch. Anterior and posterior ceratohyals (Fig. 5d) connected by narrow or broad sutures; anterior ceratohyal narrow an-

teriorly lacking a "beryciform" foramen. Branchiostegal rays six, four associated with anterior ceratohyal, two with posterior.

Premaxilla with well-developed ascending process and an expansive and complex process articulating with maxilla; alveolar ramus with a large dorsal flange centrally.

Suspensorium with cartilagenous articulations. Hyomandibular a narrow strut ventrally, flanged dorsally with an anterodorsal condyle, articulating with prootic and sphenotic, and a truncate dorsal facet articulating with pterotic. Broad metapterygoid articulating anteriorly with quadrate, anterodorsally with endopterygoid, ventrally with rod-like symplectic, and posterodorsally with hyomandibular. Endopterygoid a broad oval with a ventrally directed truncate process; articulating anteroventrally with ectopterygoid and posterior palatine, ventrally with quadrate and posteriorly with metapterygoid. Symplectic not contacting hyomandibular. Palatine with a tooth-bearing shelf ventrolaterally; prepalatine with an elongate process articulating with maxilla.

Neurocranium robust and convex in profile around the extremely large orbital region. A large myodome opening to brain cavity behind orbit. Supraoccipital and parietal-epiotic crests prominent. Ethmoid pointed anteriorly and relatively narrow, its lateral flanges folded ventrally. Lateral ethmoid with a large foramen; anterior and posterior lamellae of lateral ethmoid divergent ventrally, straddling palatine articulation, articulating also with frontal, supraethmoid, parasphenoid, and vomer; vomerine articulation with lateral ethmoid narrow, leaving a foramen medially. Frontal much curved over orbit with a deep fossa between supraorbital crest and sagittal crest or broad medial ridge; sensory canal of frontal enclosed in bone. Supraoccipital broad, crest-bearing portion projecting well forward between posterior extensions of frontal and posteriorly to very near foramen magnum. Parietal small, its dorsolateral ridge bearing a well developed crest in adults. Occipital with crest continuous with parietal and produced into spine posterolaterally. Pterotic with lateral ridge angulate, deflected ventrally behind orbit, more-or-less rounded above hyomandibular articulation, not produced into a spine; sensory canal enclosed in bone, with opening to supratemporal canal at angle of pterotic ridge; pterotic modified posteriorly in some species to form anterodorsal portion of a large fossa (saccular fossa) overlying saccular region (Fig. 6b). Sphenotic angulate, deflected ventrally behind orbit and moderately produced posteriorly; a large facet ventrally forming dorsal portion of articular surface for hyomandibular condyle; a foramen present in dilatator groove behind lateral process. Prootic forming rear of orbit, ventral margins of myodome, and anterior floor of cranium. Dorsally a large facet on prootic forming ventral portion of hyomandibular condyle articular surface. Trigemino-fascialis bridge of prootic well developed; four foramina usually present in trigemino-fascialis region near edge of myodome; posterior prootic little modified (Fig. 6a) or greatly folded to form anterior portion of saccular fossa (Fig. 6b). Pterosphenoid roughly kidney-shaped in outline articulating with frontal, prootic and sphenotic and separated medially by wide myodome. Orbitosphenoid lacking. Basisphenoid small, a thin shaft basally with divergent flanges dorsally, not articulating with adjacent bones. Intercalar absent. Exoccipital expansive, articulating with prootic, pterotic and epiotic anteriorly, supraoccipital dorsally, parasphenoid and basioccipital ventrally. Exoccipitals meeting dorsomedially and posteromedially, thus framing foramen magnum; posterior aspects meeting at angle creating two condylar surfaces for atlas vertebra; ventral portion of exoccipital bone little modified or forming much of dorsal portion of saccular fossa (Fig. 6a, b); three foramina present, presumably corresponding to glossopharyngeal, vagal and occipital nerves (Allis,



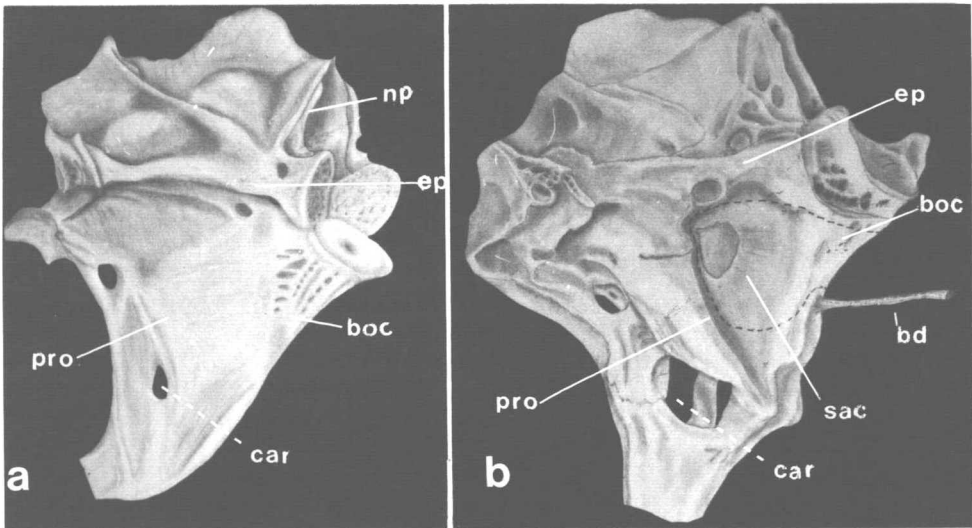


Figure 6. Left posterolateral aspect of skulls in a) *Heteropriacanthus cruentatus*, b) *Priacanthus arenatus*, with selected features noted: ep (epiotic bone), pro (prootic bone), boc (basioccipital bone), car (carotid foramen), np (autogenous neural process of first vertebra), sac (sacculus), bd (Baudelot's ligament). First vertebra remains fused to skull in b.

1909). A small foramen present or absent at exoccipital-epiotic-pterotic joint in floor of temporal groove. Sacculus (if present) sometimes incompletely ossified (Fig. 6b). Sagitta roughly round to ovoid with a deep, slightly S-shaped median sulcus and coarse crenulations on margins (Fitch and Crooke, 1984, fig. 8). Basioccipital flared, forming posterior floor of posterior myodome and articulating with exoccipital dorsally, prootic anteriorly, and parasphenoid antero-ventrally; articular facet for atlas vertebra at about 60° angle to those of exoccipitals. Parasphenoid a narrow straight shaft anteriorly, angling sharply upward behind orbit and flaring posteriorly to form anterior floor of posterior myodome which is not open posteriorly; a small to large carotid foramen at parasphenoid-prootic joint (Fig. 6a, b). Baudelot's ligament attaching to parasphenoid behind prootic joint. Vomer relatively broad, broadly pointed anteriorly and bearing oblique tooth patches, coalescing medially in adults.

Myological configuration and ligamenture of jaw region consisting of relatively broad, roughly rectangular,  $A_1$  component of adductor mandibulae muscle, occupying dorsal three-fifths of cheek cavity, subdivided into two approximately equal components ( $A_{1a}$  and  $A_{1b}$  of Winterbottom, 1974?).  $A_1$  originating on preopercle posteroventral to orbit and bounded anteriorly by dorsal half of maxilla-mandibular ligament which inserts dorsally near tip of maxilla.  $A_2$  component of adductor mandibulae a broad trapezoidal muscle occupying ventral three-fifths of cheek cavity (overlain in part dorsally by  $A_1$ ) originating posteriorly on preopercle and, deeper, on hyomandibular, and bounded anteriorly by ventral half of maxilla-mandibular ligament, which is continuous anteriorly with posterior ligament of relatively large  $A_w$  muscle inserted into Meckelian fossa of dentary. Differentiated  $A_3$  component, with an origin on lateral surface of bones underlying cheek cavity (quadrate, symplectic and others), apparently not present. A conspicuous thick, narrow to broad ligament extending from subocular shelf of third

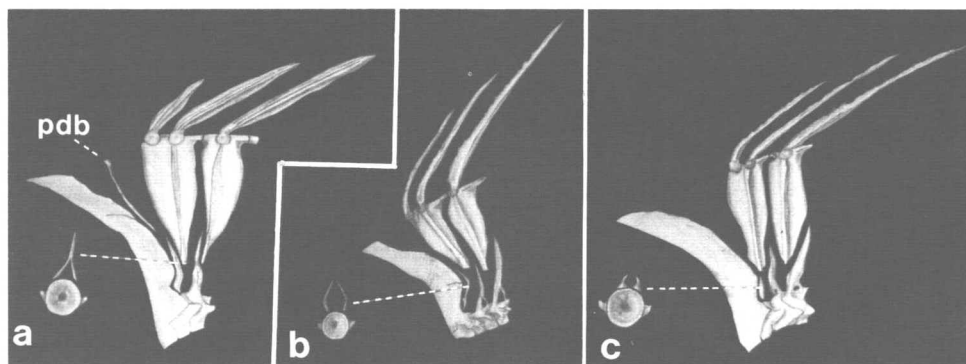


Figure 7. Bones of nuchal region (left view), including predorsal bone (pdb), in: a) *Pristigenys alta*, b) *Cookeolus japonicus*, c) *Heteropriacanthus cruentatus*.

infraorbital to dorsal surface of ectopterygoid bone above adductor mandibulae complex.

Vertebrae 10+13, the first fused to basi- and exoccipitals in large adults; first neural processes autogenous from vertebra and fused to foramen magnum in large adults, fusing dorsomedially to form a spine or not (Fig. 7a–c). Pleural ribs on third to tenth vertebrae, posterior ribs narrowly or broadly flanged (Fig. 5f). Epipleurals on ribs of third to seventh or eighth vertebrae. Epineurals at first and second vertebrae. First haemal spine relatively thin, of moderate length and not bound to anal pterygiophores, or massive, lengthened and strongly bound to pterygiophores (Fig. 8a, b). Caudal vertebrae with posterior zygapophyses fused to haemal spines, forming lateral foramina or not (Fig. 8a, b).

Principal caudal rays 8+8; procurent rays 3–5+3–5; procurent spur lacking. Three epurals. Two pair of uroneurals, the second a narrow sliver, occasionally not present. Five hypurals (third and fourth sometimes fused); parhypural with a large hypurapophysis.

Predorsal bones 0 or 1. Two spines on first dorsal and anal proximal pterygiophores. First dorsal pterygiophore between first and second vertebrae. Predorsal formulae 0+2/1/1/1/ or 2/1/1/1/.

Pectoral girdle with cleithrum very elongate and little curved. Single postcleithrum with a thin ventral shaft and a narrow lobe dorsally. Supracleithrum serrate, with or without large posterior process dorsally (Fig. 5g) and not bearing a portion of lateral-line canal dorsally. Two radials inserting on scapula, one at scapular-coracoid interspace, second at coracoid. Baudelot's ligament attaching to supra-cleithrum medially.

Pelvic bones lying between cleithra and extending well anterior to pectoral girdle; pelvic bones with a narrow or broad ventral flange (Fig. 5e). Postpelvic processes narrow or expanded into lobes (Fig. 5c).

Swimbladder simple, with posterior extensions only, or with both posterior and anterior extensions (Fig. 9a–c), the latter associated with saccular fossae of skull (Fig. 6b). Extrinsic swimbladder muscles present or absent; if present, originating on first rib and inserting on anterior or anteroventral aspect of swimbladder (Fig. 10a–c). Intestine of moderate length with three bends overlying right side of stomach; pyloric caecae of moderate length or long, length about 4–9 times thickness, about 8–13 in number. Gonads tubular or broadly triangular.

Larvae (Caldwell, 1962b; Leis and Rennis, 1983) deep-bodied, laterally com-



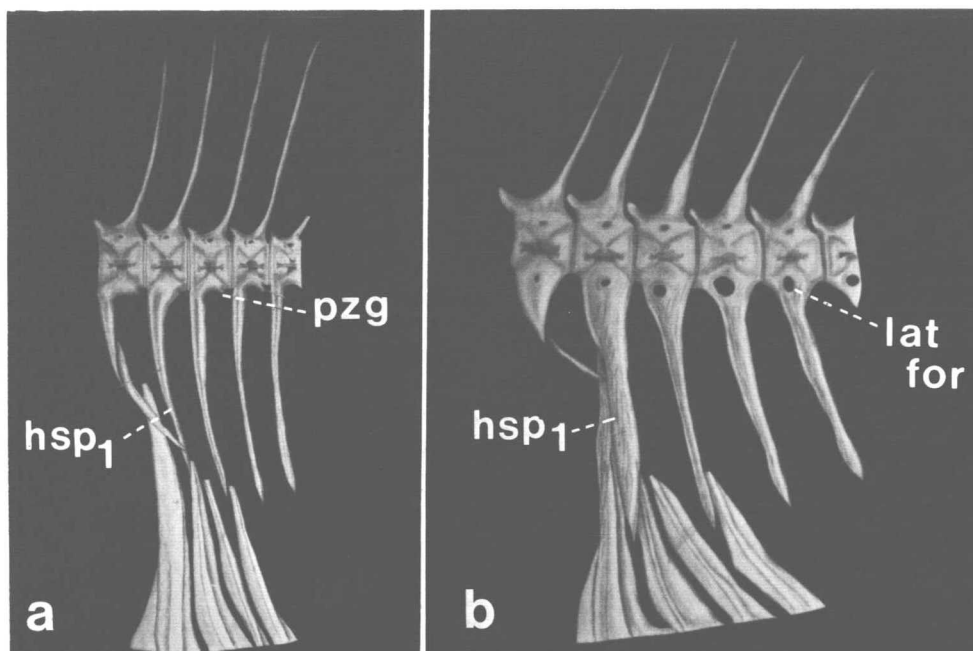


Figure 8. Anterior caudal vertebrae, showing condition of first haemal spine (hsp<sub>1</sub>), posterior zygapophyses (pzg) and lateral foramina (lat for), and proximal anal pterygiophores of: a) *Pristigenys alta*, b) *Priacanthus sagittarius*.

pressed, with 23–25 myomeres; head relatively broad, mouth large, reaching middle of large orbit. At 2–20 mm TL, a conspicuous supraoccipital crest present, with a smooth (in smallest larvae) to serrate posteriorly directed spine which projects well over dorsum. Prominent serrations on supraorbital area and lower jaw; preopercle with prominent tripointed spine at posteroventral angle, middle point long, smooth to serrate, reaching anal fin at maximum development, receding with maturity. Small interopercular, posttemporal, supracleithral and opercular spines present. Fin spines and rays serrate in 10–20 mm specimens. Scales beginning from minute precursors with oblique spiny projections, fully formed at about 20 mm TL. For further details of development see Leis and Rennis (1983) and Johnson (1984).

#### KEY TO THE SPECIES OF THE FAMILY PRIACANTHIDAE

- |   |                                    |
|---|------------------------------------|
| 1a. Anal soft rays 10–11; dorsal soft rays 11–12; scales in lateral series 36–51 (genus <i>Pristigenys</i> )  | 2                                  |
| 1b. Anal soft rays 13–16; dorsal soft rays 12–15; scales in lateral series 56–115   | 5                                  |
| 2a. Dorsal soft rays 12; anal soft rays 11; midlateral scales with about 8–20 spinules on posterior margin; sides of adults, in life, with narrow, red bars (western Pacific) |                                    |
|   | <i>Pristigenys meyeri</i> p. 138   |
| 2b. Dorsal soft rays 11; anal soft rays 10; mid-lateral scales with about 24–42 spinules on posterior margin; sides of adults lacking narrow, red bars                        | 3                                  |
| 3a. Total gill rakers on first arch 27–29; sides often with distinct white bars in both juveniles and adults (Indo-Pacific)   |                                    |
|   | <i>Pristigenys nipponia</i> p. 140 |
| 3b. Total gill rakers usually 23–27; sides of larger specimens (over 75 mm SL) usually with white bars indistinct   | 4                                  |
| 4a. Scales in lateral series 42–45; gill rakers usually 25–26; midlateral scales with about 35–50 spinules posteriorly (Fig. 2a) (western Atlantic)                           |                                    |
|   | <i>Pristigenys alta</i> p. 134     |

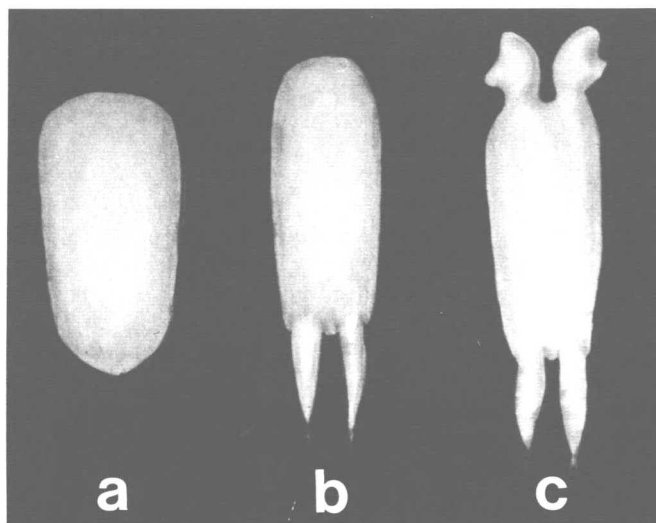


Figure 9. Swimbladder configurations (dorsal view) of: a) *Pristigenys* and *Cookeolus*, b) *Heteropriacanthus*, c) *Priacanthus*.

- 4b. Scales in lateral series 45–51; gill rakers usually 23–24; midlateral scales with about 25–32 spinules posteriorly (Fig. 2b) (eastern Pacific) ..... *Pristigenys serrula* p. 141
- 5a. Scale rows between dorsal-fin origin and lateral line 16–20; pelvic fins very long in all except largest specimens (over 300 mm SL), greatly exceeding head length; preorbital bone (lacrymal) with large serrations anteriorly (Fig. 5a) (circumtropical) ..... *Cookeolus japonicus* p. 145
- 5b. Scale rows between dorsal-fin origin and lateral line usually fewer than 16; pelvic fins shorter, usually less than to slightly exceeding head length in specimens up to 300 mm SL (larger specimens uncommon); preorbital bone with fine serrations anteriorly (Fig. 5a) (except in *Priacanthus tayenus* which has large black spots on pelvic membranes lacking in *Cookeolus*) ..... 6
- 6a. Posterior preopercle (behind sensory canal) lacking scales and notably striate; membranes of soft dorsal and anal fins and caudal fin with rows of elliptical dark specks (may be absent in eastern and central Atlantic specimens); anterior profile nearly symmetrical, the extremity of lower jaw about even with midline of body (circumtropical) ..... *Heteropriacanthus cruentatus* p. 150
- 6b. Posterior preopercle scaled behind sensory canal; dorsal, anal and caudal fins lacking dark specks [larger, faint dusky spots (yellow-brown in life) in dorsal and anal fins only of preserved specimens of *Priacanthus macracanthus*]; anterior profile asymmetrical, extremity of jaw above or below midline of body (genus *Priacanthus*) ..... 7
- 7a. Pelvic-fin membranes with several large purplish black spots; dorsal soft rays usually 12 (rarely 13); midlateral scales of specimens over 75 mm SL lacking spinules (Fig. 3c) (western Pacific and northern Indian oceans) ..... *Priacanthus tayenus* p. 180
- 7b. Pelvic-fin membranes lacking black spots or with a single basal spot; dorsal soft rays usually 13 or more; midlateral scales with spinules (except in most adults of *P. sagittarius*, Fig. 3h) ..... 8
- 8a. Pelvic fins lacking a black spot at the base; preopercular spine (sometimes broken) usually reaching to or well beyond opercular margin in specimens of all sizes ..... 9
- 8b. Pelvic fins with a black spot at the base; preopercular spine usually not reaching to opercular margin or completely obsolescent in specimens over 100 mm SL ..... 10
- 9a. Dorsal-, anal- and pelvic-fin membranes with yellow-brown spots (gray in preservative); soft portions of dorsal anal fins not distinctly whiter posteriorly; body not tapering from just behind head (western Pacific and eastern Indian oceans) ..... *Priacanthus macracanthus* p. 169
- 9b. Dorsal-, anal- and pelvic-fin membranes lacking spots; soft portions of dorsal and anal fins creamy white on posterior half; body generally tapering from just behind head (Indo-Pacific) ..... *Priacanthus fuchi* new species p. 164

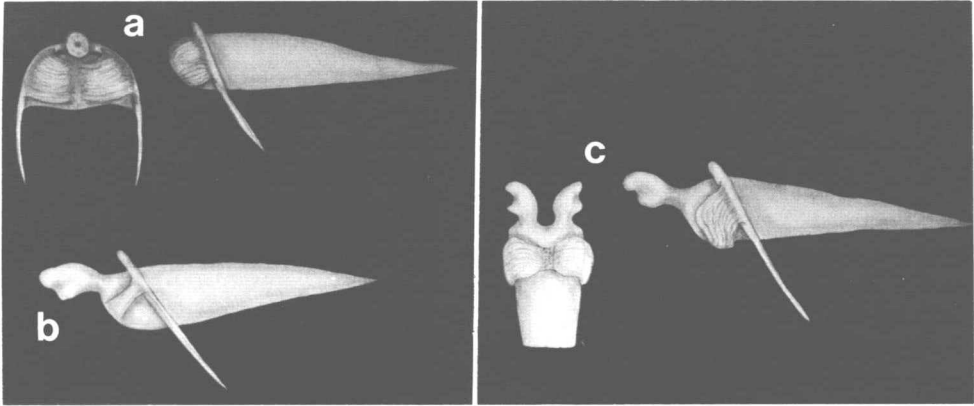


Figure 10. Extrinsic swimbladder muscles of: a) *Heteropriacanthus cruentatus* (anterior and left lat. views), b) *Priacanthus hamrur* (left lat. view), c) *Priacanthus tayenus* (ventral and left lat. views).

- |   |   |
|---|---|
| 10a. Caudal-fin margin concave; soft anal-fin rays usually 15–16 .....  | 11  |
| 10b. Caudal-fin margin truncate to convex, or slightly emarginate; soft anal-fin rays usually 14 or less .....  | 14  |
| 11a. Scales in lateral series 104–120 (Hawaiian Is.) .....  | <i>Priacanthus meeki</i> p. 172                   |
| 11b. Scales in lateral series 96 or fewer .....   | 12  |
| 12a. Total gill rakers on first arch usually 24–26 (Indo-Pacific) .....   | <i>Priacanthus hamrur</i> p. 166                  |
| 12b. Total gill rakers on first arch usually 29–32 (rarely 28) .....  | 13  |
| 13a. Body depth at sixth dorsal spine goes about 2.9–3.1 in standard length (northwest Indian O., possibly to western Pacific) .....  | <i>Priacanthus prolixus</i> new species p. 175    |
| 13b. Body depth at sixth dorsal spine goes about 2.6–2.8 in standard length (Atlantic; probable undescribed form from Galapagos Is. may key here) .....   | <i>Priacanthus arenatus</i> p. 159                |
| 14a. Total gill rakers on first arch 25–28; pectoral fins bright yellow in life (Japan, Philippine Is.) .....   | <i>Priacanthus zaizerae</i> new species p. 183    |
| 14b. Total gill rakers 23 or fewer; pectoral fins not yellow in life .....  | 14  |
| 15a. First two spinous dorsal-fin membranes with black blotches; length of second dorsal spine about twice in tenth spine; scales in lateral series 67–74 (Red Sea and Reunion to Samoa) .....      | <i>Priacanthus sagittarius</i> new species p. 178 |
| 15b. First two spinous dorsal-fin membranes without blotches darker than succeeding membranes; length of second dorsal spine 1.5–1.7 in length of tenth spine; scales in lateral series 72–93 ..... | 15  |
| 16a. Length of pectoral fin about 1.9–2.2 in head length (measured from tip of upper jaw to tip of opercular spine) (Gulf of Aden to Samoa) .....   | <i>Priacanthus blochii</i> p. 162                 |
| 16b. Length of pectoral fin goes about 1.3–1.6 in head length .....   | 16  |
| 17a. Scales in lateral series 72–84 (Hawaiian Is. and eastern Pacific) .....  | <i>Priacanthus alalaua</i> p. 155                 |
| 17b. Scales in lateral series 89–94 (Easter I.) .....   | <i>Priacanthus nasca</i> new species p. 173       |

### Genus *Pristigenys* Agassiz

*Pristigenys* Agassiz, 1835: 299 (type species, *Chaetodon substriatus* Blainville, 1818: 352, a fossil, by subsequent designation of White, 1936).

*Pseudopriacanthus* Bleeker, 1869: 241 (type species, *Priacanthus nipponius* Cuvier, 1829, by subsequent designation of Morrison, 1889).

**Diagnosis.** — Deepest bodied, yet most robust, members of Priacanthidae, occurring in tropical and tropically influenced seas except for eastern and southern Atlantic (Fig. 11). Broadly ovate in profile; maximum overall width at preopercles; body relatively thick, maximum width immediately behind opercles. External sexual dimorphism not evident. The following morphological conditions which vary within Priacanthidae, according to the family description, serve to distinguish

Recent *Pristigenys* from other priacanthid genera. Scales of head region most modified of family, those of chin, gular area and top of head much modified (Fig. 1) and exposed resulting in extremely rough texture. First to fifth branchiostegal rays with well-developed scales over most of length. Scales present on preopercle posterior to sensory canal. Body scales relatively large (36–51 in lateral series). Scales of midlateral region broadly rounded posteriorly with about 8–50 spinules along posterior margin (Fig. 2a–c); anterior scale margin truncate; scale circuli with microscopic denticles (Fig. 4a). Spinous portion of dorsal fin rounded, fourth to sixth spines longer than seventh to ninth, tenth about as long as fifth in large adults; soft portions of dorsal and anal fins broadly pointed, 11–12 and 10–11 rays respectively. Pectoral fins relatively short and broadly pointed, subequal in length to pelvic spine. Caudal fin rounded. Pelvic fins inserted beneath pectorals, of moderate length in Recent species, reaching to or beyond anal fin origin in young, falling short in some large adults. Spinules lost from spines of all fins in adults; spinules present on basal three-fourths of soft dorsal and anal rays, basal one-third of pectoral rays and basal two-thirds of pelvic soft rays. Shelf overlying sensory canal of preopercles prominent and serrate overall; sensory canal mostly open posteriorly; preopercular spine completely obsolescent in adults. Interopercle with a single, blunt posterior process. Nasal bones deeply spoon-shaped with serrate ridges on anterior process. Teeth on dentary about 70–75, on vomer 90–100, on palatine 90–100+, premaxilla 180–200. Pseudobranchs with about 50–60 filaments. Lacrymal and second infraorbital with spines and coarse serrations anteroventrally (Fig. 5a), becoming somewhat obsolescent with age. Gill rakers on first arch 23–29. Anterior and posterior ceratohyals joined by a narrow suture (Fig. 5d). Frontal bones meeting to form a broad ridge with no sagittal crest. Bones overlying saccular regions of skull not modified to form deep fossae, appearing generally as in *Heteropriacanthus* (Fig. 6a). Neural processes of first vertebra fused dorsomedially to form spine (Fig. 7a). Pleural ribs lacking broad flanges as in *Priacanthus* (Fig. 5f); epipleurals present on ribs of third to eighth vertebrae. First haemal spine relatively thin, not greatly elongate nor bound to anal pterygiophores (Fig. 8a). Posterior zygopophyses of caudal vertebrae not fused to haemal spines to form lateral foramina (Fig. 8a). Procurent caudal rays 3+3. Single predorsal bone present (Fig. 7a). Supracleithrum without large posterior process dorsally (Fig. 5g). Posterior pleural ribs with narrow flanges as in *Priacanthus* (Fig. 5f). Pelvic bone with a relatively narrow ventral keel (Fig. 5e); postpelvic processes expanded into lobes (Fig. 5c). Swimbladder simple (Fig. 9a), lacking anterior or posterior extensions, strongly attached laterally and dorsolaterally to ribs of third to seventh vertebrae 3–7. Extrinsic swimbladder muscles not present. Pyloric caecae 7–8, moderately long, length 5–6 times thickness. Gonads elongate, tubular. Soft portions of dorsal and anal fins and caudal fin with black marginal band.

*Remarks.* — The nomenclature of the group here referred to as *Pristigenys* has been controversial with respect to the nominal genus *Pseudopriacanthus*. Agassiz (1835) listed *Pristigenys substriatus* (without description) as a new combination for *Chaetodon substriatus* Blainville (1818), a fossil species of the Eocene Monte Bolca Formation in Italy, first erroneously reported by Volta (1796) as the present-day species, *Chaetodon striatus*. Agassiz later (1839) provided a short redescription of this form and considered it to be a genus near *Beryx*. As a consequence it was listed in the Berycidae in the classifications of fossils of Woodward (1901) and Eastman (1905). Bleeker (1869) described the genus *Pseudopriacanthus* to include *Priacanthus niphonius* Cuvier (1829). Morrison (1889) formally designated this species as the type of the genus and also allocated *Priacanthus altus* Gill and *P.*

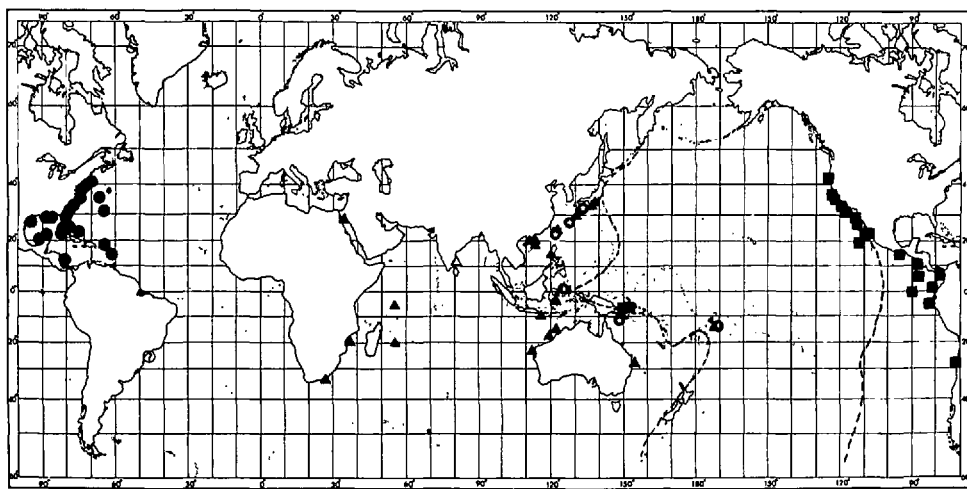


Figure 11. Distributions of species of the genus *Pristigenys*: *P. alta* (circles), *P. niphonia* (triangles), *P. meyeri* (circled stars), *P. serrula* (squares) (dashed lines demarcate approximate margins of Pacific Tectonic Plate). Asterisks denote records based on pelagic postlarvae; open symbols are questionable records.

*meyeri* Günther (as a synonym of *niphonius*) to the group as did Boulenger (1895). White (1936) first noted the similarity of the genera in question, synonymized them, and thus finally transferred *Pristigenys* from Berycidae to Priacanthidae. After being overlooked by several authors in intervening years, Myers (1958) noted and concurred with this arrangement and emended the gender of species epithets in his short review of the group, followed by Smith (1966).

Fitch and Lavenberg (1975) suggested that *Cookeolus* Fowler should be synonymized with *Pristigenys* based on the common possession of long pelvic fins by the fossil species *P. substriata* and the Recent species *Cookeolus japonicus*. Fritzsche (1978) stated that there was no evidence to support the synonymy of *Pristigenys* with any extant priacanthid genus but, later (in Fritzsche and Johnson, 1981), reversed this view based on osteological comparison, citing primarily the common possession of a predorsal bone and similar fin meristics in the fossil and extant forms. Fitch and Crooke (1984) took considerable issue with this position and contended that *Pseudopriacanthus* was a valid genus based on the fact that *Pristigenys* had several characters intermediate between extant genera, including scale size, body shape and fin lengths, and also cited the fossil species' probable pelagic (vs. epibenthic?) habitat as further evidence for its distinctness from present-day genera.

The rigorous osteological comparison of present-day priacanthids conducted in this study facilitates an analysis of the status of *Pristigenys*. The Monte Bolca fossils are in excellent condition. Examination of clear photographs and drawings of *P. substriata* (BMNH P.16370) revealed that the trunk skeleton, all visible features of the skull, and outline of the body are essentially identical to those of present-day species here allocated to *Pristigenys*, the only differences being the longer pelvic fins and slightly longer median fins. It clearly lacks the osteological conditions herein considered derived and diagnostic for other priacanthid genera, such as absence of the predorsal element, greatly enlarged first haemal spine, expanded pelvic girdle flange, and sagittal crest on frontals. *Pristigenys substriata*

is thus hypothesized to be in the phyletic lineage including species formerly allocated to the nominal *Pseudopriacanthus*. Considering the magnitude of differences between other priacanthid genera recognized herein, the possession of longer fins, and possibly different sized scales (not confirmed here), are hardly valid criteria for the recognition of an additional genus if levels of recognition across groups are to be meaningful.

*Pristigenys alta* (Gill)

Plate Ia; Figures 1, 4a, 5a, c-e, g, 7a, 8a, 9a, 12a, 13

*Priacanthus altus* Gill, 1862: 132 (Narragansett Bay, R.I.).

**Diagnosis.**—A member of the *Pristigenys alta* species group here distinguished from *Pristigenys meyeri* by scale type (form and number of spinules on lateral scales of adults, about 8–20 in *meyeri*, 25–50 in *alta* group, Fig. 2a–c), by lack of narrow red bars, presence of broad orange bars separated by narrow white bars, and fewer dorsal soft rays (11 vs. 12) and fewer anal soft rays (10 vs. 11). Within *alta* group, distinguished from Indo-Pacific *P. niphonia* by fewer total gill rakers on first arch (modally 26 vs. 29) and, in adults, usually less distinct white bars. Distinguished from *P. serrula* of the eastern Pacific by fewer scales (42–45 vs. 45–51 in lat. series), more spinules on posterior scale margins in adults (35–45 vs. 24–32, Fig. 2a, b), higher gill raker counts (modally 26 vs. 24), and several aspects of ontogenetic shape change (Fig. 14), including that of caudal peduncle, orbit and interorbit, and soft dorsal fin length.

**Description.**—Based on 20 specimens, dorsal-fin rays X, 11 (rarely 10 or 12, Caldwell, 1962); anal-fin rays III, 10; pectoral-fin rays 17–18 (16–19). Scales in lateral series 42–45 (43.1), lateral-line scales 36–40 (37.5); vertical scale rows 37–46 (40.7), 9–12 rows above lateral line, 26–34 below. Midlateral scales with about 35–45 (fewer in small juveniles) spinules posteriorly as in *P. niphonia* (Fig. 2a). Total gill rakers on first arch 24–28 (25.8), 17–20 on lower arm, 7–8 on upper.

General profile evident in Plate Ia. Maximum known size 261 mm SL. Body proportions are based on 10 specimens 54.0–236.0 mm SL. BD 484–630 (534), BW 190–233 (211), CPL 140–174 (159), CPD 111–129 (119), HL 357–405 (385), HD 410–415 (466), HW 228–253 (245), ORB 197–218 (208), IO 064–102 (082), SNT 090–104 (046), JW 216–258 (242), D1L 169–252 (202), D2L 219–255 (239), AL 209–244 (230), P1L 198–256 (224), P2L 280–447 (351). Significant ontogenetic variation in several morphometric distances accounts for much of the wider ranges listed here. Chief among these are relative decreases in body and head depths and dorsal-spine and pelvic fin lengths with growth. Body profile nearly orbicular in younger specimens (Fig. 12a), becoming more elongate-ovate with maturity. Pelvic fins reaching past anal spines in young but barely reaching or failing to reach first anal spine in adults.

Color in life of adults and subadults dark red (pink to orange just after preservation) on body, head and fins; iris of eye red and/or silvery (Caldwell, 1962a). Some preserved specimens show evidence of faint, light bars not as distinct as in *P. niphonia*. Black margins on soft portions of dorsal and anal fins and caudal fin; black confined to extreme edges in larger adults. Pectoral fins clear to slightly pink; distal one-third of pelvic fins black; membranes of spinous portion of dorsal fin dusky along anterior edges of spines. Some specimens on preservation may show faint blotching in median fins and oblique bars on soft portion of dorsal fin.





Plate I. a) *Pristigenys alta*, 90 mm SL, Gulf of Mexico, photo R. L. Shipp; b) *Pristigenys nipponia*, 180 mm SL, Japan, photo H. Masuda; c) *Pristigenys serrula*, about 250 mm SL, Baja California, photo J. W. Schott; d) *Pristigenys meyeri*, 235 mm SL, Japan, photo H. Masuda; e) *Cookeolus japonicus*, 211 mm SL, Baja California, photo P. Gregory; f) *Cookeolus japonicus*, 276 mm SL, Easter Island, photo J. E. Randall; g) *Cookeolus japonicus*, about 350 mm SL, Revillagigedo Islands, photo L. Stockland; h) *Priacanthus fitchi*, new species 162 mm SL, Western Australia, photo G. Leyland.

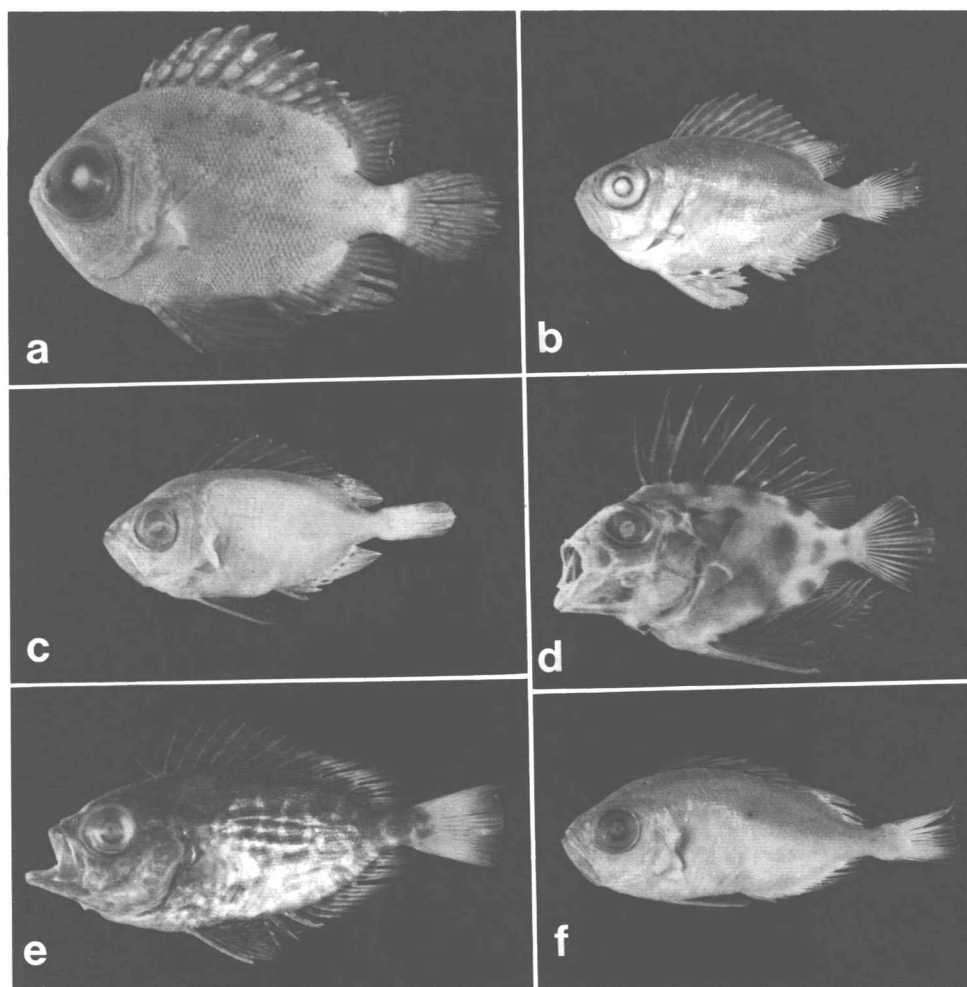


Figure 12. Pelagic juvenile specimens of: a) *Pristigenys alta*, 27 mm SL (USNM 58892); b) *Priacanthus tayenus*, 24 mm SL (USNM 182715); c) *Priacanthus sagittarius*, 31 mm SL (ANSP 151675); d) *Cookeolus japonicus*, about 12 mm SL (from transparency of South Carolina Mar. Res. specimen photoed by G. D. Johnson); e) *Heteropriacanthus cruentatus*, 53 mm SL (USNM 240085); f) *Priacanthus macracanthus*, 41 mm SL (ANSP 151678).

Prejuveniles and juveniles (Figs. 12a, 13; Caldwell, 1962b, figs. 11–20) silvery gray in pelagic stages, red after transformation to benthic stage. In very young, spinous portion of dorsal fin black (sometimes with honeycomb pattern), except for tips of spines and central row of light spots centered on spines which become larger and orange with age; a second row of light spots forming distal to these at 20–30 mm SL, coalescing with first and fin becoming mostly clear of medial dark pigment in specimens 50–60 mm SL. Soft portions of dorsal and anal fins with black pigment basally from origin to about ninth ray, pigment receding anteriorly with maturity, disappearing at about 20 mm SL; larger specimens (30–50 mm SL) with dark specks on soft rays of dorsal and anal fins and with ragged bands near bases which migrate distally with maturity to form marginal bands at about



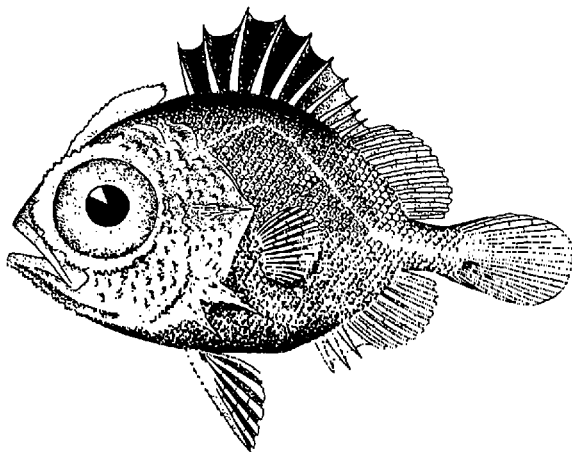


Figure 13. Pelagic postlarval specimen of *Pristigenys alta*, 7.5 mm SL (drawn for Bureau of Fisheries, H. L. Todd, 1886).

60 mm SL. Caudal fin with specks and blotches mostly on rays, which also migrate ontogenetically to form posterior marginal band. Pelvic fins mostly black, the spines spotted or banded, dark pigment decreasing with age and confined to distal one-third in specimens about 100 mm SL.

*Distribution.* — Western Atlantic in Caribbean, Gulf of Mexico and along east coast of North America (Fig. 11); postlarvae are transported northward in Gulf Stream currents and juveniles are commonly recorded as far north as southern New England waters (Bean, 1903; Schroeder, 1938) and are known from Maine (Scattergood and Coffin, 1957). Very small pelagic stages are recorded from Gulf Stream waters off Bermuda (Matthews et al., 1977). No large adults are known from north of Cape Hatteras (Caldwell, 1962b), and thus juveniles probably do not survive over winter in more northerly latitudes. A single specimen (SU 68163), an old exchange specimen from MNHN (pers. comm., M. E. Anderson), is putatively recorded from Brazil. Based on the strictly Caribbean and northward distribution of all other specimens, that locality is believed to be in error. Ribeiro (1961) reported *P. alta* from Brazil but the data and illustration given clearly represent *Cookeolus japonicus*. There are no other records from South American or eastern Atlantic waters.

*Biological Notes.* — Occurs at depths of from about 5 to 125 m as transformed juveniles and adults (Caldwell, 1962b) where they are usually solitarily associated with rocks and burrows (Parker and Ross, 1986) and are possibly territorial (Shipp and Hopkins, 1978). Larvae and postlarvae are pelagic and are especially common along the western margin of the Gulf Stream in late summer. Off southern Florida, spawning is believed to occur in shallow habitats from mid-July to mid-September (Caldwell, 1962b). Transformation from pelagic to juvenile stage occurs over a size range of about 35–55 mm SL, with the age at settling apparently dependant upon suitable habitat.

*Remarks.* — *Pristigenys alta* and *P. serrula* of the eastern Pacific are phenetically very similar. However, there are clear and consistent differences in meristic and morphometric characters. *P. alta* has significantly (based on standard *t*-tests) lower

average counts of scales in lateral series (43.1 vs. 48.1,  $t$  Stat. = 5.53), lateral line (37.5 vs. 40.3,  $t$  Stat. = 3.69), and vertical rows (40.7 vs. 43.2,  $t$  Stat. = 1.79). Total gill raker counts are significantly higher in *alta* (25.8 vs. 23.8,  $t$  Stat. = 3.55). Counts of spinules on midlateral scales of adults are non-overlapping, being higher in *alta* (about 33–45 vs. 25–32). An analysis of morphometric features shows clear ontogenetic differences between Atlantic and Pacific populations. Comparative plots of measurements relative to standard length revealed divergence in several, with the chief ones being caudal peduncle depth, which becomes relatively greater in *serrula*, orbit diameter which is greater in *alta* with corresponding decreases in interorbital distance, and soft dorsal-fin length which is greater in *alta*. Principal components analysis performed on logs of measurements (Fig. 14) clearly reflected these differences in ontogenetic shape change with adults of Atlantic and Pacific samples clearly separating along PC II (PC I is principally size-related), while juveniles group together. Heaviest factor loadings along PC II were for same distances discussed above. The complete separation of adult specimens along a horizontal axis indicates that these differences are probably not confounded by size.

The type specimen of *Pristigenys alta* is apparently no longer extant but the taxon's identity is obvious from Gill's (1862) original description.

*Material Examined.* — 173 specimens, 3–261 mm SL. ATLANTIC OCEAN OFF BERMUDA (pelagic postlarvae): USNM 194484,2; USNM 282902,1; USNM 282903,1; USNM 282904,1; USNM 282905,1; USNM 282906,2. BAHAMAS: USNM 282868,1. BERMUDA: ANSP 103967,1; ANSP 134145,1. BRAZIL?: SU 68163,1. CUBA: USNM 5330,1; USNM 84498,4; USNM 117086,1; USNM 186468,2. FLORIDA: CAS 20585,1; CAS 48457,1; SU 2800,1 USNM 132201,1; USNM 134165,1; USNM 181345,1; USNM 186130,1; USNM 186471,1; USNM 186472,1; USNM 204950,1; USNM 282864,2; USNM 282885,1; USNM 37772,1; USNM 73063,1; USNM 84511,1. GEORGIA: LACM 42730-22,2; USNM 190413,1; USNM 204948,3; USNM 204950,1; USNM 282866,1; USNM 282877,1; USNM 282880,1; USNM 282881,1. LESSER ANTILLES: AMNH 28364,1. LOUISIANA: USNM 179725,1. MASSACHUSETTS: CAS 20584,3; USNM 126831,1; USNM 15583,1; USNM 20642,1; USNM 43732,3; USNM 49618,1; USNM 49664,6; USNM 49665,1; USNM 55831,22 (2 C&S); USNM 58832,1; USNM 58833,2; USNM 58892,6; USNM 63928,1; USNM 68129,4; USNM 85780,1. MISSISSIPPI: USNM 155625,1 C&S; NEW JERSEY: AMNH 20073,2; AMNH 20320,1; AMNH 3238,1; USNM 45456,1. NEW YORK: AMNH 12130,1; AMNH 12520,1; AMNH 15779,1; AMNH 18339,1; AMNH 19478,1; AMNH 20639,1; AMNH 2237,1; AMNH 4477,1; AMNH 8293,1; USNM 10763,1. NICARAGUA: USNM 187974,3. NORTH CAROLINA: USNM 111795,2; USNM 111796,1; USNM 111797,2; USNM 151917,1; USNM 282865,1; USNM 282889,11; USNM 282892,4; USNM 292890,1; USNM 292893,18. RHODE ISLAND: CAS 20583,1; USNM 178351,3; USNM 37377,1. SOUTH CAROLINA: CAS 10409,1; USNM 187976,3; USNM 204948,3. VIRGINIA: USNM 155612,1; USNM 155627,1. LOCALITY UNKNOWN: USNM 175221,1; USNM 273066,3 C&S.

*Pristigenys meyeri* (Günther)  
Plate Id; Figure 2c

*Priacanthus meyeri* Günther, 1871: 656 (Celebes).

*Pristigenys multifasciata* Yoshino and Iwai, 1973: 61 (Ryukyu Is.).

*Diagnosis.* — A member of *Pristigenys* distinguished from other members of genus (*alta* species group) by the presence in life of narrow red bars on the head and body, by having 12 (vs. 11) dorsal soft rays and 11 (vs. 10) anal soft rays, and by scale type (midlateral scales with about 8–20 large spinules on posterior margin vs. 24 or more smaller spinules in other species) (Fig. 2a–c).

*Description.* — Includes data of Yoshino and Iwai (1973) except where noted as “(2 specs.)”: dorsal-fin rays X,12; anal-fin rays III,11; pectoral-fin rays 18–19 (17–

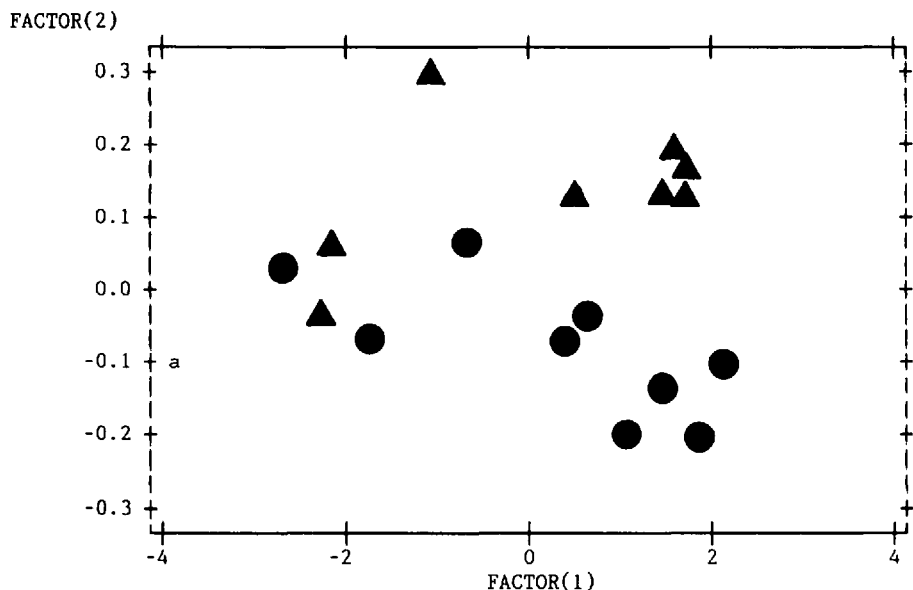


Figure 14. Graphed results of principal components analysis of morphometric distances for *Pristigenys alta* (circles) and *P. serrula* (triangles).

19). Scales in lateral series (2 specs.) 38. Lateral-line scales 30–33 (31.3). Vertical scale rows (2 specs.) 37–39, 9 above lateral line, 27–29 below. Scales of midlateral area with 8–20 spinules on posterior margin (Fig. 2c). Total gill rakers on first arch 23–25 (23.9) (17 on lower arm, 7 on upper in 2 specimens).

General profile evident in Plate Id. Maximum known size 225 mm SL. Body proportions are based on two available adult specimens 215 and 225 mm SL. BD 542–555, BW 251–262, CPL 139–149, CPD 121–122, HL 391–413, HD 513–533, HW 288–291, ORB 231–232, IO 056–071, SN 106–115, JW 266–269, D1L 198–215, D2L 200–231, AL 226–251, P1L 232–245, P2L 342–348. Juvenile specimens not available and general patterns of ontogenetic variation are unknown but may be similar to congeners.

Color in life (based on illustrations in Masuda et al., 1984 and others) yellowish pink with 10 or more narrow red bars on body and head interspersed by intermittent red markings. Cheeks, maxilla and snout with red vermiculations; iris of eye red. Fins reddish; dorsal spines creamy; soft dorsal and anal fins and caudal fin with black margins; pectoral fins clear or pinkish; distal one-third of pelvic fins black; membranes of spinous portion of dorsal fin dusky anterior to spines. Coloration of juveniles is unknown. Dark fin pigmentation may follow an ontogenetic pattern similar to that in other members of the genus, as adult phases are essentially identical. Patterns of juvenile body and head pigmentation cannot be speculated upon as the adult pattern is very different from other *Pristigenys* species.

*Distribution.*—Thus far known only from the western Pacific Ocean (Fig. 11); recorded from Japan, South China Sea, Sulawesi, New Guinea and Samoa. Confined to Indian-Australian and Eurasian tectonic plate regions except on margin of the Pacific Plate at Samoa.

*Biological Notes.*—All specimens for which data are available have been collected in rocky areas at 100–200 m depth. Nothing is known of the early life history of *P. meyeri*. The smallest specimen reported by Yoshino and Iwai (1973) is 189 mm SL.

*Remarks.*—*Pristigenys meyeri* is clearly the most distinctive member of the genus differing markedly in pigmentation patterns, scale morphology and meristic characters from the three members of the *alta* species group. Despite this distinctness, the species has been synonymized with *P. nipponia* since the work of Bleeker (1873b) and thus redescribed by Yoshino and Iwai (1973) who had not seen the type of *meyeri*. These authors did note that Günther's (1871) species had 12 soft dorsal and 11 soft anal rays but dismissed this similarity based on his description of uniform red coloration. Günther, however, saw the type specimen long after preservation and the color description was probably based on his conception of general coloration in priacanthids. Examination of the type of *meyeri* reveals the unmistakable scale morphology described herein for *meyeri* and by Yoshino and Iwai for *multifasciata* rendering the forms synonymous.

Yoshino and Iwai (1973) stated a branchiostegal ray count of 7 (specimens not seen by me); however, in two specimens examined (including the type of *meyeri*) the counts are 6, the usual complement in all members of Priacanthidae.

*Material Examined.*—SULAWESI: BMNH 1871.7.20:46,1: 215 mm SL (holotype). SAMOA: BPBM 27766,1.

### *Pristigenys nipponia* (Cuvier)

#### Plate Ib; Figure 2a

*Priacanthus nipponius* Cuvier, 1829: 107 (Japan).

*Myripristis refulgens* Valenciennes, 1862: 1169 (Seychelles).

*Diagnosis.*—A member of *Pristigenys alta* species group distinguished from *P. alta* by having higher gill raker counts (modally 29 vs. 26) and usually much more distinct light vertical bars on body. Distinguished from *serrula* of the eastern Pacific by higher gill raker counts (27–29 vs. 23–25) and more spinules on midlateral scales of adults (about 40–45 vs. 25–32). Distinguished from the partially sympatric Indo-Pacific species *P. meyeri* by the lack of red bars, fewer soft dorsal and anal rays (11 vs. 12, 10 vs. 11), and scale type (see *P. meyeri* diagnosis).

*Description.*—Based on 20 specimens, dorsal-fin rays X, 11 (rarely 10 or 12); anal-fin rays III, 10; pectoral-fin rays 18–19. Scales in lateral series 42–49 (45.2); lateral-line scales 37–43 (39.7); vertical scale rows 38–45 (40.7), 9–12 above lateral-line, 28–32 below. Scales of midlateral area with about 40–50 spinules (fewer in small juveniles) on posterior margin (Fig. 2a). Total gill rakers on first arch 27–29 (28.3), 19–20 on lower arm, 8–9 on upper.

General profile evident in Plate Ib. Maximum known size 274 mm SL. Body proportions are based on 10 specimens 67–190 mm SL. BD 529–612 (573), BW 231–247 (239), CPL 148–170 (155), CPD 122–129 (126), HL 359–388 (379), HD 473–606 (503), HW 235–254 (244), ORB 184–221 (202), IO 082–097 (090), SNT 084–104 (097), JW 238–266 (252), D1L 181–224 (205), D2L 195–241 (214), AL 206–239 (222), P1L 213–243 (229), P2L 316–386 (354). Patterns of ontogenetic morphometric variation generally as described for *P. alta* with substantial reductions in body and head depth and pelvic fin lengths with maturity.

Color of adults (Plate Ib) dark red to reddish orange on head, body and fins;

iris of eye red to silvery; 4 or 5 light bars on head and body, becoming narrower with maturity; first bar at dorsal fin origin, extending to bottom of opercle, second beneath fifth dorsal spine extending to belly, third beneath ninth dorsal spine extending to first anal spine, and fourth and fifth at anterior and posterior caudal peduncle. Dorsal-fin spines and anterior portions of membranes creamy pink, posterior portions of membranes dusky. Soft portions of dorsal and anal fins and caudal fin with black margins and light submarginal bands in adults and subadults. Pectoral fin clear or slightly pink; distal one-third of pelvic fins black or dusky. Young specimens of a range of sizes show same ontogenetic patterns of dark pigmentation described for *P. alta*.

*Distribution.* — Western Pacific and Indian Oceans (Fig. 11); Queensland and Western Australia northward to southern Japan. Kailola's (1974) record from Papua New Guinea has subsequently been reidentified as *P. meyeri*. In Indian Ocean, known from South Africa, Mozambique Channel, Reunion and Seychelles (Smith, 1966) and questionably India (Day, 1875). In Red Sea at Eilat, Israel (A. Diamant, in litt.). Not known to occur on Pacific Plate except from postlarval specimen taken at Samoa.

*Biological Notes.* — Associated with rocky habitats and known from 80 to 100+ m depth but probably occurring in shallower depths as well, especially as juveniles. Eggs are pelagic, small (0.75) and spherical (Leis and Rennis, 1983). The Samoan postlarval specimen was collected in December.

*Remarks.* — Smith (1966) cast doubt on the distinctness of *P. nipponia* from *P. serrula* of the eastern Pacific. Clear differences stated here, including non-overlapping gill raker counts, lower scale counts, and more spinules on the midlateral scales in *nipponia* leave little doubt as to the distinctness of these species. These species are also apparently allopatric by several thousand kilometers.

*Material Examined.* — 47 specimens, 5–274 mm SL. CHINA: CAS 19753,1. EAST CHINA SEA: CAS 13611,1. JAPAN: AMNH 26817,1; AMNH 3977,3; CAS 55036,1; CAS 55038,4; CAS 55042,1; CAS 55043,1; CAS 55044,1; MCZ 49689,1; SU 18190,1; SU 23997,1; USNM 151682,1; USNM 151851,1; USNM 161417,1; USNM 22536,1; USNM 57544,1; USNM 57582,1; USNM 59686,1. PHILIPPINES: CAS 32882,1; CAS 34187,1; CAS 52588,1; CAS 53444,1. QUEENSLAND: QM 18825,2. SOUTH CHINA SEA: CAS GVF 1765,1; CAS GVF 1766,6; CAS GVF 1768,1. SAMOA: USNM 276112,1 (postlarva). SEYCHELLES: MNHN 2590,1: 274 mm SL (type of *Myripristus refulgens*). TAIWAN: CAS 30319,1; SU 49392,1; SU 49394,1; USNM 282876,2. WESTERN AUSTRALIA: WAM P.25923-003,1; WAM P.26217-006,1.

### *Pristigenys serrula* (Gilbert)

Plate 1c; Figure 2b, d

*Priacanthus serrula* Gilbert, 1891: 450 (Panama Bay).

*Pseudopriacanthus lucasanus* Clark, 1936: 388 (Cabo San Lucas, Baja California).

*Diagnosis.* — A *Pristigenys* of the *alta* species group distinguished from group member *P. nipponia* of Indo-Pacific by having higher scale counts (LS  $\bar{x}$  = 48.1 vs. 45.8), fewer gill rakers (23–25 vs. 27–29), and fewer spinules on midlateral scales of adults (about 25–32 vs. 40–50), and in less distinct white bars on sides. Distinguished from *P. alta* of western Atlantic by higher scale counts (LS 45–51 vs. 42–45), fewer gill rakers (modally 24 vs. 26), fewer midlateral scale spinules in adults (25–32 vs. 35–45, Fig. 2a, b), and in several aspects of ontogenetic shape change as noted in "Diagnosis" and "Remarks" under *P. alta*.

*Description.*—Based on 19 specimens, dorsal-fin rays X,11 (rarely 10); anal-fin rays III,10; pectoral-fin rays 17–18. Scales in lateral series 45–51 (48.1); lateral-line scales 40–45 (43.2); vertical scale rows 39–44 (42.5), 11–13 above lateral-line, 28–32 below. Scales of midlateral area in adults with about 25–32 spinules posteriorly. Total gill rakers on first arch 23–25 (23.8), 16–17 on lower arch, 7–8 on upper.

General profile evident in Plate Ic. Maximum known size 274 SL (Fitch and Crooke, 1984). Body proportions are based on 10 specimens 74.7–255.0 mm SL. BD 507–585 (543), BW 188–237 (208), CPL 153–175 (164), CPD 117–137 (130), HL 353–402 (373), HD 444–514 (473), HW 212–244 (231), ORB 170–207 (184), IO 080–098 (088), SNT 088–111 (098), JW 225–254 (236), D1L 157–238 (196), D2L 170–254 (222), AL 189–254 (219), PIL 203–253 (226), P2L 288–469 (349). General patterns of ontogenetic morphometric variation are as discussed for *P. alta* but see differences under “Remarks” of that species.

Life colors and ontogenetic development of pigmentation patterns as described for *P. alta* based on a complete size-range of specimens. One subadult specimen (176 mm SL) shows evidence of extremely vague light bars positioned as in *P. niphonia* (Pl. Ib); such bars are not known to be boldly exhibited as in *niphonia*.

*Distribution.*—Eastern Pacific along continental shelf of North and South America and offshore islands (Fig. 11); apparently common along Mexican and Central American coasts and recorded from Galapagos and Revillagigedo Islands; uncommonly collected in California waters north to Monterey Bay but, in El Niño years (1982–1983), in apparent response to warming trends, adults have been recorded from central California to Newport, Oregon (R. N. Lea, in litt.). Known along coast of South America from Ecuador (Orces, 1959), Peru (Hildebrand and Barton, 1949), and, as adults, from Antofagasta, Chile (Alberti, 1963; Kong et al., 1981).

*Biological Notes.*—Known to occur at depths of fewer than 5 to over 100 m in rocky habitats.

*Remarks.*—Gilbert's (1891) description of *P. serrula* was based on a small juvenile specimen (38.8 mm SL) from the Pacific coast of Panama. He made no comparisons to the similar *P. alta* of the western Atlantic, apparently presuming allopatric speciation had occurred. Data presented herein clearly support separate species status for Atlantic and eastern Pacific *Pristigenys* populations (see “Remarks” under *P. alta*). See also “Remarks” under *P. niphonia*.

*Material Examined.*—44 specimens, 36–255 mm SL. BAJA: CAS 2708,1: 56.7 mm SL (holotype of *Pseudopriacanthus lucasanus*); CAS 13423,1; CAS 13423,2; CAS 17621,1; CAS 36610,5; CAS 40409,1; CAS 40410,1; CAS 40411,1; CAS UNCAT.,1; LACM 34194-1,1; LACM 34244-1,2; LACM 34245-1,1; LACM 34246-1,1; LACM 35723-1,1; LACM 38669-1,1; LACM W68-24,1. CALIFORNIA: CAS 20577,1; CAS 40409,1; CAS 52604,1; CAS 52604,1; CAS 54923,1; CAS 54923,1; CAS 54924,1; CAS 54924,1; CAS UNCAT.,1; LACM 30820-1,1; LACM 30835-1,1. COCOS ISLAND: LACM 32280-2,1. EL SALVADOR: USNM 282878,1. GULF CALIFORNIA: CAS 55039,2; LACM 35739-31,3; LACM 35742-24,1. OAXACA: LACM 22796,1; SU 37470,1. PANAMA: USNM 43407,1: 38.3 mm SL (holotype). PERU: USNM 144265,1.

### Genus *Cookeolus* Fowler

*Cookeolus* Fowler, 1928: 190 (as a subgenus of *Priacanthus* Oken, elevated to generic status by Fowler, 1947: 1) (original type-species *Anthias boops* Schneider in Bloch and Schneider, 1801, by original designation; subsequent type species *Priacanthus japonicus* Cuvier 1829, designated herein).

*Diagnosis.*—Monotypic circumtropical genus containing largest species of Priacanthidae. Exceeding 500 mm SL; deep bodied and laterally compressed; young broadly ovate in profile, adults elongate-ovate; most distinguished by extremely long pelvic fins in all but largest adults. External sexual dimorphism not evident. The following morphological conditions which vary within Priacanthidae serve to distinguish *Cookeolus* from other priacanthid genera. Scales relatively small, 60–83 in lateral series. Scales of head region much modified, very slightly less so than those of *Pristigenys* (Fig. 1). Scales present posterior to shelf overlying sensory canal of preopercle. Scales present on first and second branchiostegal rays. Scales of midlateral area rounded to broadly pointed posteriorly with 25–35 spinules on margin (Fig. 2h); anterior margin truncate; posterior (apical) field slightly elevated and supported medially by centrally protruding flange. Scale circuli corrugate (Fig. 4b). Spinous dorsal fin of graduated height, increasing posteriorly, tenth spine much longer than others. Soft portions of dorsal and anal fins relatively long and broadly pointed, greatly exceeding eye diameter except in largest specimens, 12–14 and 12–13 rays respectively. Caudal fin rounded. Pectoral fins of moderate length, broadly pointed, shorter than pelvic spines in all except largest specimens. Pelvic fins very long in young (Fig. 12d), extending to middle of caudal fin in smaller juveniles, allometrically decreasing in growth rate (Fitch and Crooke, 1984, fig. 5), not reaching anal fin origin in very large adults (>400 mm SL); pelvic fins inserted well anterior to pectorals. Spinules present anteriorly on first to third dorsal spines, second and third anal spines, and over all of ventral surface of pelvic spines of adults; spinules present on basal one-third of soft dorsal, anal and pectoral-fin rays and basal one-half of pelvic-fin soft rays. Shelf overlying sensory canal of preopercle little pronounced, finely serrate overall; canal mostly closed with small elongate openings posteriorly and ventrally; preopercle spine serrate basally, smooth near tip, remaining well developed in adults, reaching to tip of subopercle. Interopercle broadly pointed posteriorly, lacking a notch. Nasal bone spatulate with serrations lacking (or weak?) on anterior shaft. Lacrymal and second infraorbital with large serrations (Fig. 5a), becoming less prominent in large adults. Teeth on dentary about 70–75, vomer 80–90+, palatine 100–120, premaxilla 180–200. Pseudobranchs with about 60–70 filaments. Gill rakers on first arch 22–27. Anterior and posterior ceratohyals joined by a broad suture as in *Priacanthus* (Fig. 5d). Frontals meeting medially to form sagittal crest. Bones over saccular regions of skull not modified to form deep fossae, thus appearing as in *Heteropriacanthus* (Fig. 6a). First neural arch with elongate processes but not fused medially to form a spine (Fig. 7b). Pleural ribs lacking broad flanges; epipleurals present on ribs of vertebrae 3–7. First haemal spine massive, elongate, interdigitating with and tightly bound to anterior anal-fin basal pterygiophores, similar to *Priacanthus* (Fig. 8b). Posterior zygopophyses of caudal vertebrae not fused to haemal spines to form lateral foramina (occasionally nearly so on tenth), thus appearing as in *Pristigenys* (Fig. 8a). Procurent caudal rays 4+4. Predorsal bone lacking (Fig. 7b). Dorsal aspect of supracleithrum with a large posterior process forming a spine in smaller specimens, broadening in very large specimens (Fig. 5g). Posterior pleural ribs with narrow flanges as in *Priacanthus* (Fig. 5f). Pelvic bones with a broad ventral keel (Fig. 5e); postpelvic processes expanded into lobes as in *Pristigenys* (Fig. 5c). Swimbladder simple (Fig. 9a), lacking anterior or posterior extensions. Extrinsic swimbladder muscles lacking. Pyloric caecae of varied length, about 5–9 times the thickness, about 11–13 in number. Gonads broadly triangular, especially in gravid females.

*Remarks.*—The type species for *Cookeolus* is herein redesignated as *Priacanthus japonicus* Cuvier (1829). Comparison of the original descriptions of the former type species, *Anthias boops* Schneider (in Bloch and Schneider, 1801), and *Labrus cruentatus* Lacepède (1801), both described from St. Helena Island, gives no indication that different taxa are involved. Yet, since the work of Boulenger (1895), these names have been associated in the literature with the two very different forms known until today as *Cookeolus boops* and *Heteropriacanthus cruentatus* (*Priacanthus cruentatus* prior to the work of Fitch and Crooke, 1984). Schneider's work was based on an unpublished manuscript of J. R. Forster treating the fauna collected on the voyages of Captain Cook in the 1770's ("Descriptiones animalium," eventually published verbatim posthumously, 1844), subsequently revised by M. E. Bloch after Forster's death, and ultimately published by Schneider (in Bloch and Schneider, 1801) following Bloch's death. Sketches of Forster's intended types were made by his son, George Forster, and others and currently reside in the British Museum (Natural History) (Whitehead, 1978). These drawings cannot be considered iconotypes since they were not viewed by Schneider but nevertheless are a clear reference to the type specimens, several of which, apparently including that of *boops*, are no longer extant.

The drawing of "*Perca boops*" of Forster (Fig. 15) indicates beyond a reasonable doubt that it does not represent the long-finned form until today regarded as *Cookeolus boops* but is referable to present-day *Heteropriacanthus cruentatus*; both forms are common at St. Helena Island and no other priacanthid species is recorded from there (Edwards and Glass, 1987). The anterior profile of the specimen drawing is distorted because of a distended urohyal region, but the length and position of the pelvic fins, lengths of dorsal, anal, and pectoral fins, course of the lateral line, scale count above the lateral line and overall body configuration virtually eliminate any referral to the long pelvic-finned form. Only very large specimens of this form (near 450 mm SL) approach the body configuration and short pelvic-fin length depicted by the sketch; however, median fin and pectoral-fin lengths remain much longer than depicted at all sizes. Moreover, so far as known, most sketches were drawn "natural size" (Whitehead, 1983), about 170 mm SL in this case, and appear possibly to have been traced around the outline of the fish. As such, the figure corresponds to present-day *H. cruentatus* resulting in the synonymy of the two forms.

The mistaken association of Schneider's *boops* with the morphological entity herein treated as *Cookeolus japonicus* was apparently made by Boulenger (1895), possibly circumstantially, in part, due to the preponderance of St. Helena specimens of this species in the BMNH collection. Cuvier's (1829) conception of the species clearly was not as such, since with a copy of Forster's sketch in hand, he based his *Priacanthus boops* account on a still extant specimen (MNHN A.3062) referable to *cruentatus*. Günther (1859) did not clearly associate the name *boops* with the long-finned species either as he states that he could not "venture to bring the fish of Valenciennes—elongated ventral fins—into the synonymy of *Pr. boops*" (i.e., *Priacanthus macropus* Val., a clear synonym of the form regarded herein as *japonicus*), but he did in fact list *macropus* in the synonymy of *boops* after all, which may have provided the impetus for Boulenger's (1895) reconciliation of the name with this species which included a lengthy synonymy of other names mostly correctly applied to the long-finned form.

Both *Anthias boops* Schneider and *Labrus cruentatus* Lacepède have been designated as type species for the monotypic genera *Cookeolus* Fowler (1928) and *Heteropriacanthus* Fitch and Crooke (1984) respectively. The descriptions of these genera clearly are tied to the different morphological entities known since Bou-



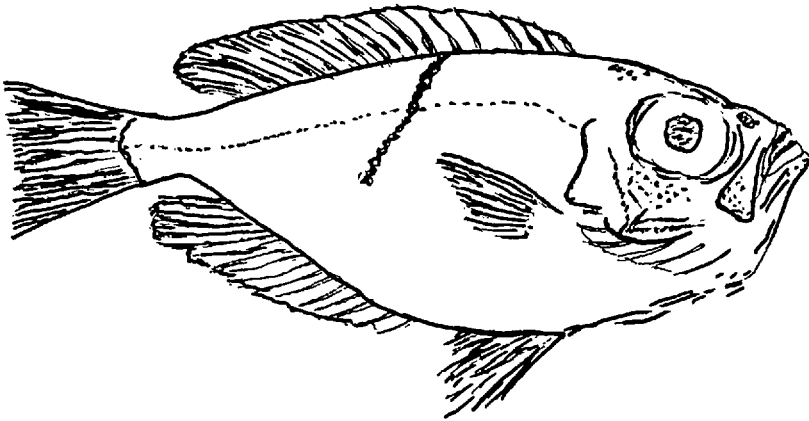


Figure 15. Drawing of "*Perca boops*" of J. R. Forster (reduced 50%) sketched by G. Forster about 1772–75.

lenger (1895) as *Priacanthus boops* and *P. cruentatus*, irrespective of the now discovered synonymy of the nominal type-species. Moreover, both species' names were published in 1801. Exhaustive searches by the author and by C. Karrer and H. Paepke in Germany failed to reveal the exact data of publication of Bloch and Schneider (1801). The publication date of Lacepède (1801) has already been rigorously established as October 16, 1801 (Roux, 1973), even though that work was often cited as "1802" by past authors.

Under Article 21 (c)(ii) of the International Code of Zoological Nomenclature, the undiscovered date of publication of Bloch and Schneider (1801) is adopted as December 31 and *boops* Schneider thus becomes a junior synonym of *cruentatus* Lacepède. A petition to the Commission on Zoological Nomenclature under Article 70 (a)(i) of the Code ("Misidentified type-species") is pending to allow redesignation of a type species for *Cookeolus*, thus preserving the stability of the genus name. *Priacanthus japonicus* Cuvier (1829) is the first clearly available name for the taxon long associated with *Cookeolus*; the type (ZMB 427) is still extant. Because of the longstanding confusion of these forms, a neotype has been designated for "*Labrus cruentatus*" Lacepède (see "Remarks" under *H. cruentatus*).

*Cookeolus japonicus* (Cuvier)  
Plates 1e–g; Figures 5e, 12d

- Priacanthus japonicus* Cuvier, 1829: 106 (Japan).
- Priacanthus macropus* Valenciennes, 1831: 469 (St. Helena I.).
- Priacanthus macropterus* Valenciennes, 1831: 471 (locality unknown).
- Priacanthus alticlarans* Valenciennes, 1862: 1168 (Seychelles).
- Priacanthus supraarmatus* Hilgendorf, 1879: 79 (Japan).
- Priacanthus velabundus* McCulloch, 1915: 114 (New South Wales).

*Diagnosis.* — As for the genus.

*Description.* — Based on 36 specimens, dorsal-fin rays X, 13 (12–14); anal-fin rays III, 13 (12–14); pectoral-fin rays 18 (17–19). Scales in lateral series 60–83 (72.7); lateral-line scales 60–73 (64.0); vertical scale rows 58–66 (62.7), 15–21 above lateral-line, 40–46 below. Total gill rakers on first arch 23–27 (24.6), 17–20 on lower arm, 5–8 on upper.

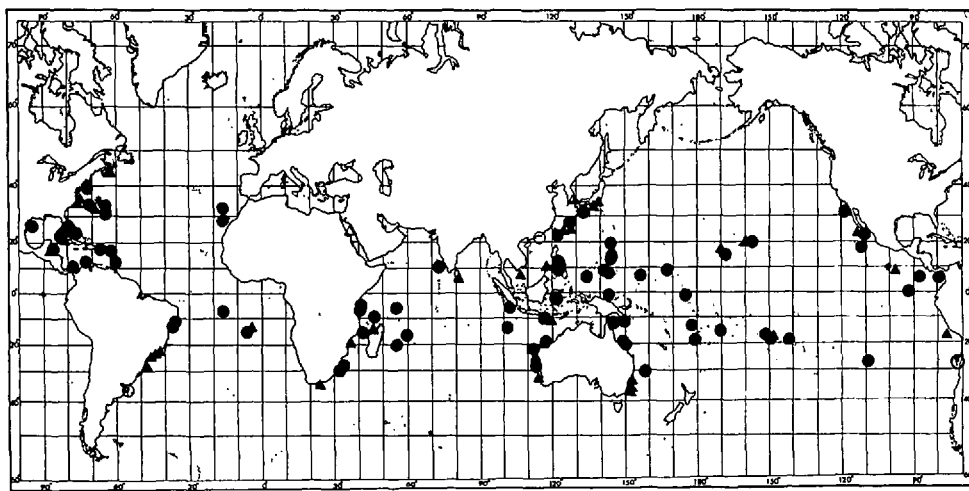


Figure 16. Distributions of *Cookeolus japonicus* (triangles) and *Heteropriacanthus cruentatus* (circles). Asterisks denote records based on pelagic juveniles. Open symbols are unsubstantiated but plausible literature records.

General profile evident in Plates Ie–g. Maximum known size 507 mm SL (Anderson et al., 1972). Body proportions are based on 36 specimens 94–492 mm SL. BD 339–557 (445), BW 133–205 (163), CPL 140–247 (169), CPD 077–139 (106), HL 252–412 (335), HD 305–479 (390), HW 146–219 (178), ORB 101–173 (139), IO 067–124 (092), SN 072–172 (097), JW 092–264 (204), D1L 102–261 (188), D2L 142–407 (257), AL 128–380 (221), P1L 163–279 (219), P2L 213–638 (383). Variation is observably great in all morphometric distances, most due to ontogenetic changes in body shape and fin lengths. The body becomes substantially more elongate with maturity (Plates If, g) which is reflected in relative decreases in body, head and caudal peduncle depths. There are also decreases in head width and orbit diameter and dramatic relative decreases in lengths of the pelvic fins and soft portions of the dorsal and anal fins (see Diagnosis) and a lesser but significant decrease in dorsal spine length. Head length, jaw and caudal peduncle length are quite variable but show no ontogenetic pattern.

Color of adults in life (based on photos) crimson to scarlet on head, body, iris of eye, and to varied degrees on fins. All fins except pectorals may be yellowish in some specimens, especially on spines and soft rays. Spinous dorsal-fin membranes black to slight dusky decreasing in intensity posteriorly. Soft portions of dorsal and anal fins and caudal fin with narrow dark fringes in subadults, disappearing in larger specimens; posterior four to five rays and membranes of soft dorsal and anal fins occasionally creamy or yellowish pink. Pectoral fins clear or pink; pelvic-fin membranes dusky to black, usually less dusky in older specimens.

Pelagic juveniles (Fig. 12d) presumably silvery in color with large dark blotches (blue or brown in life?) on body, spinous portion of dorsal fin, and anteriorly on soft portions of dorsal and anal fins; posterior soft portions of dorsal and anal fins apparently clear. Complete patterns of ontogenetic color change are not known.

*Distribution.*—Circumglobally distributed in tropical and tropically influenced seas (Fig. 16) occurring most commonly in insular habitats. Known in the western Atlantic as far north as Virginia and New Jersey (Reid, 1944; Fowler, 1947) and rarely as juveniles, to Nova Scotia (MacKay and Gilhen, 1973); pelagic juveniles

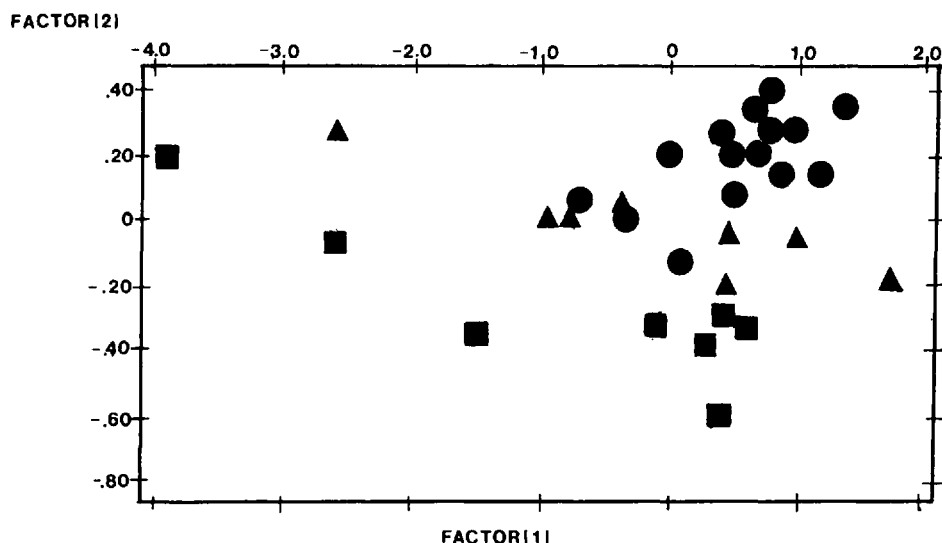


Figure 17. Graphed results of principal components analysis on morphometric distances in populations of *Cookeolus japonicus*: Indo-Pacific (squares), eastern Pacific (circles), Atlantic (triangles).

are recorded from stomachs of tuna caught northeast of Bermuda (Matthews et al., 1977). Found in southern Atlantic to Brazil (Ribiero, 1961, as "*Pseudopriacanthus altus*"), and probably Argentina. Abundant at St. Helena Island (Edwards and Glass, 1987) but no substantiated records in eastern Atlantic from African coastal or Canary Islands region. In Indo-Pacific from South Africa and south-eastern Australia north to Japan and Korea and through central Pacific islands; questionably in Red Sea (Randall 1983). In eastern Pacific from Baja California (Fitch and Schultz, 1978; Fritzsche, 1978) to Peru (Parin and Abramov, 1983).

*Geographic Variation.*—There apparently is significant geographic variation between *Cookeolus* populations on a broad regional basis. Based on a relatively small amount of material, specimens from the Indo-West Pacific ( $N = 9$ ) exhibit different regimes of allometric change in fin lengths and aspects of body shape from eastern Pacific ( $N = 15$ ) and Atlantic ( $N = 9$ ) population samples. Results of principal components analysis performed on logs of distance measurements reveal clear separation (Fig. 17) of adult and larger juvenile Indo-West Pacific specimens from those of other regions along PC II; Atlantic specimens are intermediate but overlapping eastern Pacific representatives. The single Hawaiian and Tahitian specimens are grouped with the Indo-West Pacific. Heaviest factor loadings along PC II are for lengths of soft portions of dorsal and anal fins, pelvic fins, and caudal peduncle length. Comparative plots of proportional distances showed divergence between populations with fin lengths of Indo-West Pacific specimens undergoing less proportional decrease in length in all cases; the caudal peduncle lengthens with maturity at a lesser rate in this population than in others. Meristic characters, which are only moderately variable geographically, do not show patterns of variation similar to those of morphometric data, with Indo-West Pacific specimens being generally intermediate to eastern Pacific and Atlantic populations.

*Biological Notes.*—Occurring at depths of 60 to over 400 m (Anderson et al., 1972) and reported to be moderately common at depths of 165–260 m (Randall

et al., 1985) in association with rocky holes and ledges. Remains of postlarvae (to 40 mm SL) have been removed from stomachs of yellowfin tuna (*Thunnus albacares*) caught in Gulf Stream waters near Bermuda in the months July to November (Matthews et al., 1977). These are probably products of spawning in the Caribbean 2–4 months previous. The lifespan of large specimens examined by Fitch and Schultz (1978) was believed to be 9 or more years. Principal prey items found by those authors were pelagic crabs.

*Remarks.*—Apparent differences in ontogenetic morphometric changes between populations of *Cookeolus*, though admittedly based on relatively small samples from some regions, are suggestive of regional distinctness. However, the circum-tropical distribution of *Cookeolus* irrespective of tectonic plate boundaries or other biogeographic regions, with populations apparently congregating about most oceanic islands as well as occurrence in continental waters, suggests that inter-regional gene flow was possible until relatively recent geologic times, though it is questionably now precluded. This question coupled with the above mentioned inconsistencies between meristic and morphometric characters have resulted in the decision not to regard *Cookeolus* as polytypic at the present.

Several authors (Boulenger, 1895; Fowler 1931; 1947; Herre, 1953 and others) have listed *Priacanthus bonariensis* Cuvier (1829) in the synonymy of the form known to them as *Priacanthus* or *Cookeolus boops*, now treated herein as *C. japonicus*, and Reid (1944) reported a specimen of *Cookeolus* from Virginia as "*Priacanthus bonariensis*." This name would have page priority over *japonicus* were they ascertained to be synonyms. However, prior to undertaking a family-wide revision of Priacanthidae, the author examined briefly the type of *bonariensis* (MNHN A.3059), a juvenile specimen with badly damaged head, now lost. Brief notes made at that time questionably refer this name to the synonymy of *Heteropriacanthus cruentatus*. It clearly does not seem referable to *Cookeolus* as there is no note or recollection of long pelvic fins which would have been salient on a specimen the size of the type (ca. 80–110 mm SL) and none are referred to in Cuvier's description.

Fowler (1931), Herre (1953) and possibly others have incorrectly listed *Priacanthus schlegelii* Hilgendorf (1879) in the synonymy of *Cookeolus*; that species is here referred to the synonymy of *Priacanthus hamrur* based on examination of the type.

*Material Examined.*—80 specimens, 9–492 mm SL. ATLANTIC OCEAN OFF BERMUDA (pelagic juveniles): USNM 282910,2; USNM 282911,2; USNM 282912,1; USNM 282913,1; USNM 282914,2; USNM 282917,2; USNM 282918,2; USNM 282938,1 C&S. BAJA (MEXICO): LACM 30340-1,1; LACM 39584-2,1; LACM 31796-2,1; LACM 38335-2,3; USNM 260547,1. BRAZIL: MZUSP 7739,1; MZUSP UNCAT.,1; MZUSP UNCAT.,1; MZUSP UNCAT.,1; MZUSP UNCAT.,1. HAWAIIAN ISLANDS: SU 13373,1. INDONESIA: USNM 263762,1. JAPAN: AMNH 13205,1; AMNH 26975,1; AMNH 34788,1; AMNH 34788,2; AMNH 34799,1; CAS 50018,1; SU 12095,1; SU 22817,2; UMMZ 142693,1; USNM 38818,1; USNM 49437,1; USNM 71136,1; USNM 75475,1; ZMB 427,1: 405 mm TL (holotype, photo); ZMB 10598,1: 92.4 mm SL (holotype of *Priacanthus supraarmatus*). NEW SOUTH WALES: AMS I.16129-001,1; AMS I.17000-001,1; AMS I.21564-001,1; AMS I.24094-001,1; AMS I.B.6868,1. NORTH CAROLINA: USNM 163714.1 OAXACA (MEXICO): LACM 30505-1,1; LACM 30506-1,1. QUEENSLAND: QM I.12129,1; QM I.20996,1. REVILLAGIGEDOS ISLANDS: CAS 46717,3; LACM 38339-1,1; LACM 38344-1,1; LACM 38345-1,4; LACM 39572-1,2; LACM 39885-1,1. SEYCHELLES ISLANDS: MNHN A.2585,1: 250 mm SL (holotype of *Priacanthus alticlairens*). SOUTH AMERICA (Atlantic): BMNH 1984.7.6: 1,1. ST. HELENA ISLAND: MNHN A.3562,1: 346 mm SL (holotype of *Priacanthus macropus*); USNM 267906,3. TUAMOTOS ISLANDS: BPBM 30925,1. VIRGINIA: USNM 120996,1. WESTERN AUSTRALIA: AMS I.2474,1; WAM P.26828-001,1; WAM P.272215-002,1; WAM P.28279-001,1. LOCALITY UNKNOWN: MNHN 985,1: 240 mm SL (holotype of *Priacanthus macropterus*).

Genus *Heteropriacanthus* Fitch and Crooke

*Heteropriacanthus* Fitch and Crooke, 1984: 310 [type-species by original designation "*Priacanthus cruentatus* (Lacepède, 1801)" (= *Labrus cruentatus* Lacepède, 1801)].

**Diagnosis.**—Monotypic circumtropical genus of Priacanthidae; laterally compressed, elongate-ovate in profile with a relatively symmetrically pointed anterior profile (more or less assymetrical in other genera). The following morphological conditions which vary within Priacanthidae serve to distinguish *Heteropriacanthus*. Scales relatively small, 78–96 in lateral series. Scales of head region least modified of family, having less prominent spinules, less erect orientation to dermis and less exposure due to relatively thick mucous layer, thus resulting in an overall less abrasive texture than in other genera; scales absent from tip of chin. Scales lacking on preopercle posterior to shelf overlying sensory canal. Branchiostegal rays 1–3 with few scales. Scales of midlateral area with posterior (apical) field broadly pointed, elevated, with 20–30 spinules along posterior margin, and overlying a separate posterior flange (Fig. 2g); anterior margin with three or four interradiat projections. Scale circuli corrugate (Fig. 4c). Spinous dorsal fin of graduated height, increasing only slightly posteriorly, tenth spine longest. Soft portions of dorsal and anal fins with 11–13 and 13–14 rays respectively, relatively short and broadly rounded, length subequal to eye diameter. Caudal fin margin slightly rounded. Pectoral fins of moderate length, subequal to pelvic spines, and broadly pointed. Pelvic fin short, barely reaching first anal-fin spine or falling short, inserted ventral to pectorals. Spinules well developed on dorsal spines 1–9, anal- and pelvic-fin spines; spinules laterally on basal one-fourth of soft dorsal rays, and basal three-fourths of anal and pelvic soft rays; spinules absent or very weak on pectoral-fin rays. Shelf overlying sensory canal of preopercle little pronounced, serrate on ventral aspect, smooth posteriorly; canal mostly closed with small elongate openings; preopercular spine broadly triangular, finely serrate, remaining well developed in adults, reaching nearly to tip of suboperculum. Interoperculum with a deep notch posteriorly. Nasal bones obliquely truncate posteriorly, anterior shaft lacking serrations. Lacrymal and second infraorbital with fine serrations as in *Priacanthus sagittarius* (Fig. 5a). Gill rakers on first arch 21–25. Pseudobranchs with about 65–75 filaments. Teeth on dentary about 20–30, vomer 40–50, palatines 20–25, premaxillary 75–85. Anterior and posterior ceratohyals joined by a broad suture as in *Priacanthus* (Fig. 5d). Frontal bones meeting medially in a sagittal crest. Bone overlying saccular regions of skull not modified to form deep fossae (Fig. 6a). Neural processes of first vertebra reduced to vestiges (Fig. 7c). Pleural ribs of vertebrae 7–9 with flanges, the ninth very expansive (Fig. 5f); epipleurals on ribs of vertebrae 3–7. First haemal spine massive, elongate, interdigitating with and bound to basal anal pterygiophores as in *Priacanthus* (Fig. 8b). Posterior zygopophyses of caudal vertebrae fused to haemal spines to form lateral foramina as in *Priacanthus* (Fig. 8b). Procurrent caudal rays 4+4. Predorsal bone lacking (Fig. 7c). Supracleithrum lacking a process dorsally, essentially as in *Pristigenys* (Fig. 5g). Pelvic bones with a large ventral keel as *Cookeolus* (Fig. 5e); postpelvic processes slightly expanded distally (Fig. 5c). Swimbladder with posterior projections, truncate anteriorly (Fig. 9b), not communicating directly with skull. Extrinsic swimbladder muscles present, inserting anteromedially on bladder and originating on first pleural rib (Fig. 10a). Pyloric caecae short, length about four times thickness, about 9–11 in number. Membranes of caudal and soft dorsal and anal fins usually with rows of elliptical dark specks.

**Remarks.**—*Heteropriacanthus cruentatus* is superficially very similar to members

of *Priacanthus*, from which it was recently removed by Fitch and Crook (1984) based primarily on swimbladder and otolith morphology; however it lacks several hypothesized derived features which define *Priacanthus* as a monophyletic group. The most salient of these are the trenchant skull and swimbladder modifications (Fig. 6). Further, *Heteropriacanthus* possesses several autapomorphies. Once monophyly is established, decisions concerning levels of recognition among hypothesized sister groups are arbitrary. The magnitude of differences between *H. cruentatus* and its hypothesized sister group, *Priacanthus* (see "Phylogenetic Analysis") is comparable to those between other priacanthid genera previously recognized and merits a comparable level of recognition if these levels are to be meaningful across groups. I therefore fully concur with Fitch and Crooke's erection of a monotypic genus for this taxon and have greatly expanded its diagnosis.

*Heteropriacanthus cruentatus* (Lacepède)

Plates IIa, b; Figures 2g, 4c, 5c, f, 6a, 7c, 9b, 10a, 12e, 15

*Labrus cruentatus* Lacepède, 16 October 1801: 452 (Martinique) (on illustration of Plumier).

*Anthias boops* Schneider, 31 December 1801: 308 (on "*Perca boops*" of J. R. Forster, unpub. m.s., subsequently pub. 1844) (St. Helena Island).

*Priacanthus cepedianus* Desmarest, 1823: 9 (Cuba).

?*Priacanthus bonariensis* Cuvier, 1829: 105 (Argentina?).

*Priacanthus carolinus* Cuvier, Valenciennes, 1829: 105 (Caroline Islands).

?*Priacanthus argenteus* Cuvier, 1829: 109 (Japan) (on illustration of Renard, Pt. I, Pl. 12, fig. 72, in d'après Corneille de Vlaming, No. 12).

*Priacanthus fulgens* Lowe, 1838: 196 (Madeira).

*Priacanthus bleekeri* Castlenau, 1873: 100 (Nob Island, northern Australia).

*Diagnosis.* — As for the genus.

*Description.* — Based on 27 specimens, dorsal-fin rays X, 13 (12–13); anal-fin rays III, 14 (13–14); pectoral-fin rays 18 (18–19). Scales in lateral series 78–96 (85.6); lateral-line scales 63–81 (69.6); vertical scale rows 56–68 (62.6), 9–12 above lateral-line, 46–56 below. Total gill rakers on first arch 21–25 (23.0), 17–20 on lower arm, 4–6 on upper.

General profile evident in Plate IIa. Maximum known size 254 mm SL. Body proportions are based on 27 specimens 101.5–254.0 mm SL. BD 378–446 (406), BW 127–181 (151), CPL 128–165 (148), CPD 087–101 (094), HL 305–341 (324), HD 249–381 (342), HW 157–187 (174), ORB 133–165 (148), IO 079–105 (093), SN 089–105 (094), JW 185–213 (200), D1L 099–145 (123), D2L 124–174 (158), AL 112–163 (147), P1L 131–203 (183), P2L 172–242 (167). There are no consistent patterns of ontogenetic variation in this species.

Color in life (based on transparencies and published photos) pink to red on head, iris of eye, body and fins; alternately (Pl. IIb), body and head often silvery, blotched with pink and/or red. Spinous dorsal-fin membranes and margin of caudal fin often dusky; membranes of caudal and soft portions of dorsal and anal fins with rows of conspicuous, elliptical dark specks, lacking in mid- and eastern Atlantic specimens examined. Pectoral fins clear to pinkish, pelvic fins whitish with light dusting of melanophores in distal two-thirds.

Pelagic juveniles (Fig. 12e) silvery, heavily blotched with dark pigment (blue in life) on head and body with two well defined dark basicaudal spots; all fins except caudal with large dark spots in membranes, often straddling rays, especially in spinous portion of dorsal fin. Transitional pigment patterns between pelagic

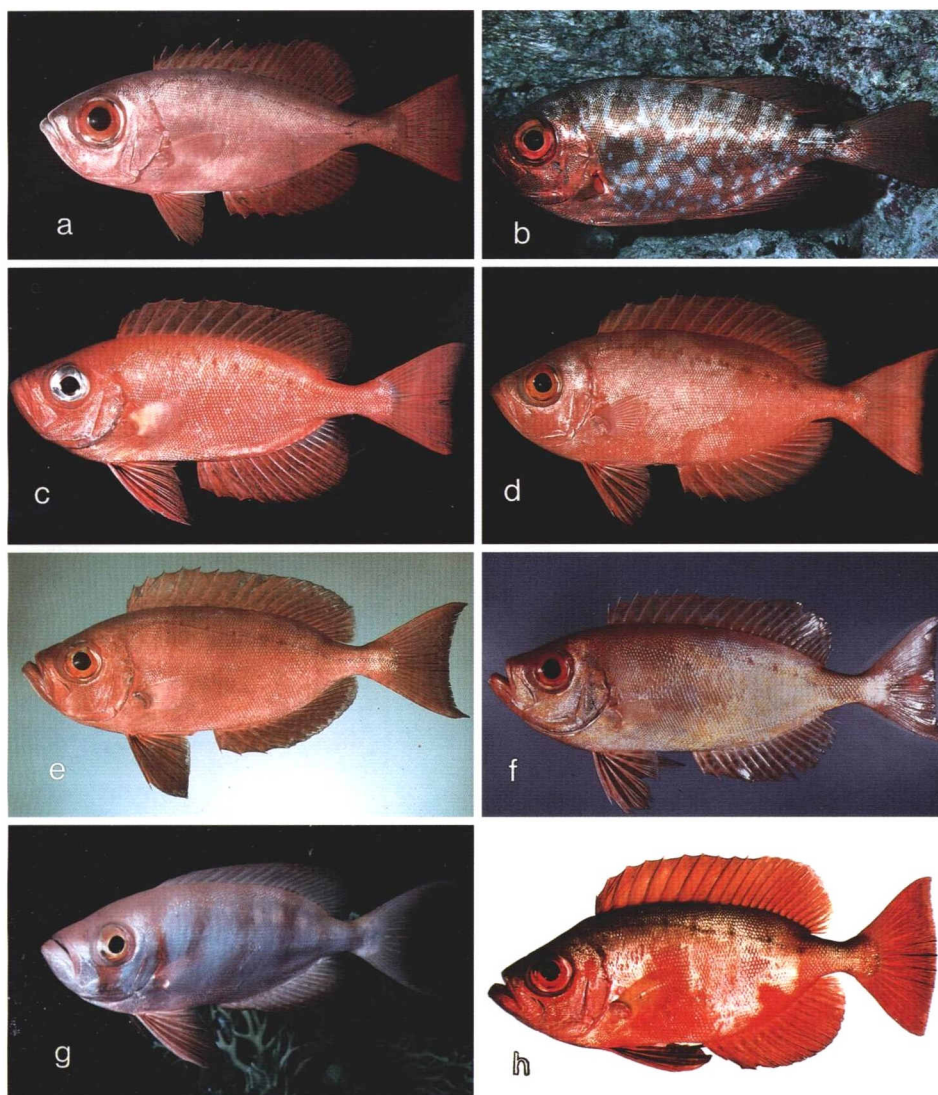


Plate II. a) *Heteropriacanthus cruentatus*, 152 mm SL, Lord Howe Island, photo J. E. Randall; b) *Heteropriacanthus cruentatus*, Eastern Island, photo J. E. Randall; c) *Priacanthus arenatus*, 212 mm SL, Virgin Islands, photo J. E. Randall; d) *Priacanthus meeki*, 236 mm SL, Oahu, photo J. E. Randall; e) *Priacanthus hamrur*, 200 mm SL, Gulf of Aqaba, photo J. E. Randall; f) *Priacanthus hamrur*, 255 mm SL, Western Australia, photo G. Leyland; g) *Priacanthus hamrur*, about 250 mm SL, Great Barrier Reef, photo J. E. Randall; h) *Priacanthus hamrur*, 200 mm SL (USNM 289289), South Africa, photo P. C. Heemstra.

and epibenthic juvenile stages are not known and are presumably of very short duration.

*Distribution.*—Circumglobal in tropical and tropically influenced seas (Fig. 16); apparently much more common in insular habitats than continental waters. In

western Atlantic, uncommonly recorded in continental waters from off Florida to Flower Garden Reef off Texas in Gulf of Mexico; a single juvenile recorded from New Jersey. Pelagic juveniles have been collected from the vicinity of Bermuda in late summer and fall months. Common in Caribbean islands and uncommon along coast of South America to Argentina. In eastern and mid Atlantic islands from Madeira to St. Helena and not definitely recorded from African continental waters. The speculative range given in Starnes (1981) may be partially in error. In Indo-Pacific, recorded from coast of South and eastern Africa, but not Red Sea, and eastward in island habitats through central Pacific. Common in island habitats of eastern Pacific from off Baja California to Galapagos; probably uncommon along coast of Mexico, Central America, and South America, questionably to Chile (Kong et al., 1981).

*Geographic Variation.*—Despite its worldwide distribution, variation in this species is remarkably minimal. Principal components analysis performed on logs of traditional and truss measurements revealed no patterns of variation, with specimen plots being virtually horizontal linear along PC I according to size. Meristic variation, though considerable in such characters as scale counts within regional samples, is negligible between regions. The only consistent regional phenomenon in the lack of dark specks in the median-fin membranes of eastern and mid Atlantic specimens. Rosenblatt and Waples (1986) reported significant allelic variation (Nei genetic distance = 0.14) between western Atlantic and eastern Pacific samples in biochemical studies of proteins and negligible variation between Hawaiian and eastern Pacific samples.

*Biological Notes.*—Inhabits shallow reef areas, primarily around islands, mostly at depths of 20 m or less. Observed to be common in both lagoon and seaward reef habitats, remaining in or near holes by day and foraging actively at night (Amesbury and Myers, 1982) and usually occurring in more shallow habitats than members of other priacanthid genera, such as *Priacanthus* (Longley and Hildebrand, 1941). Hiatt and Strasburg (1960) believed that this species also feeds, at least opportunistically, during daytime hours. Chief food items represented several feeding habitats and included octupi, pelagic shrimp, stomatopods, crabs, small fish and polychaetes. Pelagic juveniles collected from the Gulf Stream off Bermuda are probably indicative of a late spring–early summer spawning season in the Caribbean region. Sound production has been documented and studied in this species (Salmon and Winn, 1966).

*Remarks.*—Because of the longstanding confusion surrounding *Labrus cruentatus* Lacepède (1801) and *Anthias boops* Schneider (in Bloch and Schneider, 1801), involving the type species of two genera (see “Remarks” in *Cookeolus* generic account), it seems prudent to designate a neotype for *Labrus cruentatus* to stabilize the identity of the type of the genus *Heteropriacanthus* Fitch and Crooke (1984). The original description is based on a poor illustration, rendered by Plumier, of a specimen from Martinique, Lesser Antilles. A specimen from an adjacent island is selected as the neotype: USNM 285473, 157 mm SL, Lesser Antilles, Dominica near South Scotts Head, V. G. Springer, 26 October 1964.

Lacepède’s written description of *Labrus cruentatus* does not distinguish between *H. cruentatus* and a second species occurring in the Caribbean, *Priacanthus arenatus*. Plumier’s illustration is of cartoon-like quality, but the rounded caudal fin, short pelvic fins and blotched color pattern illustrated favor the taxon here regarded as *cruentatus* sufficiently to preserve these long utilized names.



*Priacanthus fulgens* Lowe (1838) has been listed in the synonymy of *Priacanthus arenatus* by some previous authors (Günther, 1859; Jordan and Evermann, 1896; Hureau, 1973). There apparently is no type extant but the description and good illustration clearly are referable to *cruentatus* based on preopercular spine, fin configurations and pigmentation.

See comments in "Remarks" under *Cookeolus japonicus* regarding the questionable referral of *Priacanthus bonariensis* Cuvier to the synonymy of *H. cruentatus*.

Edwards and Glass' (1987) listing of "*Priacanthus* n. sp. Starnes, MS" is based on a very aberrant specimen of *H. cruentatus* from St. Helena Island (ZMUC P.4432) which was earlier misconstrued as probably representing a new taxon.

*Material Examined.*—401 specimens, 28–254 mm SL. ARGENTINA: MNHN A.3059,1:80–100 mm SL (type of *Priacanthus bonariensis*). ASCENSION ISLAND: USNM 282871,1. ATLANTIC OCEAN OFF BERMUDA (pelagic juveniles): USNM 194468,1; USNM 194468,1; USNM 194469,2; USNM 194469,2; USNM 240080,1 C&S; USNM 240081,5; USNM 240082,4 (2 C&S); USNM 240083,1; USNM 240085,6; USNM 240086,8. AUSTRAL ISLANDS: AMNH 13558,1. BAHAMA ISLANDS: AMNH 17411,1; AMNH 21247,1; AMNH 21464,5; AMNH 23170,9; AMNH 23350,1; AMNH 24127,3; AMNH 24165,1; AMNH 24766,6; AMNH 25030,1; AMNH 26103,1; AMNH 27169,1; AMNH 28176,1; AMNH 28373,1; AMNH 29227,1; LACM 6753-1,3; USNM 38450,1. BELIZE: USNM 276154,1. BERMUDA: USNM 178808,1. BRAZIL: CAS 1596,1; USNM 43305,1. CANARY ISLANDS: AMNH 56157,1; AMNH 56158,1; AMNH 56159,1; MNHN A.3064,1. CAROLINE ISLANDS: CAS 50012,1; CAS 50013,1; CAS GVF 100,1; CAS GVF 111,1; CAS GVF 1385,2; CAS GVF 162,3; CAS GVF 50,1; CAS GVF 70,2; CAS GVF 835,1; CAS GVF 891,1; CAS GVF 897,1; MNHN A.168,1 3075,1; 184 mm SL (holotype of *Priacanthus carolinus*). COCOS ISLAND (Costa Rica): LACM 32254,2; LACM 32283,2; LACM 35469-42,3; LACM 3871,2; SU 6483,3. COCOS-KEELING ISLAND: ANSP 134661,2. CUBA: CAS 18418,2; MNHN A.3075:1 156 mm SL (holotype of *Priacanthus cepedianus*); SU 10326,1; USNM 110724,1 (skel); USNM 110725,1 (skel); USNM 12535,1 (skel); USNM 282929,1 (skel); USNM 2977,1; USNM 35075,1; USNM 9790,1. CURACAO: CAS UNCAT.,1. EASTER ISLAND: BPBM 6627,1; BPBM 6628,1. FIJI ISLANDS: USNM 282898,1; USNM 282899,2; USNM 282900,3. FLORIDA: AMNH 16851,1; UF 26242,1; UF 16137,2; USNM 61118,1; USNM 61119,4; SU 8194,1. GALAPAGOS ISLANDS: CAS 3692,3; LACM W67-34,1; SU 12654,1; SU 12655,1; CAS 39309,1. GILBERT ISLANDS: USNM 167389,6; USNM 167390,2; HAITI: AMNH 18968,1; AMNH 37106,4; USNM 133709,1. HAWAIIAN ISLANDS: AMNH 17411,1; ANSP 51370-78,9; ANSP 77621,1; ANSP 88776,1; ANSP 90506,1; ANSP 97861,1; CAS 10345,1; CAS 10346,1; CAS 10377,1; CAS 391,1; CAS 48151,1; LACM 309,2; MCZ 65016,1; MCZ 21946,3; SU 13371,1; SU 13372,1; SU 30496,2; SU 32104,4; SU 7772,5; USNM 125511,1; USNM 151571,2; USNM 151618,1; USNM 282861,1; USNM 282862,1; USNM 282873,1; USNM 282874,2; USNM 51089,1; USNM 52661,1; USNM 55470,1; USNM 55521,1; USNM 88188,3. INDONESIA: USNM 154090,1; USNM 282933,1; USNM 282936,1. JAMAICA: AMNH 36443,1; SU 4876,1. JOHNSTON ISLAND: LACM 3738,1; LACM 3970,2. KENYA: RUSI 11117,1. LESSER ANTILLES: AMNH 33586,1; AMNH 36693,1; LACM 7850,1; USNM 120761,1; USNM 183435,3; USNM 282856,2; USNM 282897,3 (1 C&S); USNM 282901,1; USNM 285473,1: 157 mm SL (neotype of *Labrus cruentatus*); 29852,1. LINE ISLANDS: BPBM 25294,1; USNM 141752,6; USNM 141753,1. LORD HOWE ISLAND: AMS I.17377-005,2. MADEIRA: AMNH 16871,1. MARIANA ISLANDS: ANSP 114695,1; LACM 3785,2; USNM 146719,1; USNM 141754,2; USNM 141755,1; USNM 141756,1; USNM 141757,1. MARSHALL ISLANDS: USNM 141758,1; USNM 142273,1; USNM 142274,1. MAURITIUS: FMNH 91359,6; RUSI 1271,2; USNM 19946,6; USNM 19951,1; USNM 282860,4; USNM 282863,1. MEXICO (Pacific coast): LACM 30853-8,1; LACM 31778-51,1; LACM 39584-3,1. MOZAMBIQUE: RUSI 11116,1. NEW GUINEA: AMNH 16561,1; USNM 282935,1. NEW JERSEY: ANSP 130302,1. "NOB ISLAND" (near Australia): MNHN A.3074:1 68 mm SL (holotype of *Priacanthus bleekeri*); MNHN B.3060,1. PANAMA (Atlantic coast): USNM 81931,1; USNM 81932,1. PHILIPPINES: CAS 29441,1; LACM 42463-2,1; LACM 42489-1,1; LACM 42491-1,1; SU 9731,1; USNM 154089,1; USNM 182700,1; USNM 182721,1; USNM 183204,1; USNM 183208,1; USNM 183209,1; USNM 183210,1; USNM 183211,1; USNM 183213,1; USNM 232033,1; USNM 232034,2; USNM 84251,1. PUERTO RICO: USNM 126442,1; USNM 128834,1. QUEENSLAND: AMS 19462-030,1; AMS I.17445-078,2; AMS I.19481-034,1; AMS I.22582-013,2. REVILLAGIGEDOS ISLANDS: CAS 1014,7; CAS UNCAT.,1; LACM 31778-51,1; LACM 31783-38,30; LACM 32097-50,1; LACM 38343-2,1; LACM 38668-1,2; SU 12355,1. SAMOA: AMNH 18020,1; SU 9031,2; USNM 52330,2. SEYCHELLES: ANSP 108324,1; ANSP 108325,1; ANSP 108327,1;

ANSP 108328,1; ANSP 108333,2; RUSI 11118,1; RUSI 11415,1. SOCIETY ISLANDS: USNM 282858,1; USNM 65994,1. SOUTH AFRICA: RUSI 11416,1; RUSI 9460,1; RUSI 9904,1; USNM 289287,2; USNM 289288,1. ST. HELENA ISLAND: MNHN A.166,2; MNHN A.3062,1; USNM 267884,1; ZMUC P4432,1. TAIWAN: BPBM 23349,1. TUAMOTOS: ANSP 51388,1; ANSP 89180,1; CAS 11981,1; SU 24552,3; SU 24609,1; SU 24729,1. WESTERN AUSTRALIA: AMS I.19700-013,1; WAM P.25818-005,1; WAM P.26664-002,1; WAM P.4541,1. ZANZIBAR: BMNH UNCAT.,1.

### Genus *Priacanthus* Oken

*Priacanthus* Oken, 1817: 1183 [latinization of the vernacular "Les Priacanthès" Cuvier, 1816, type species, *Anthias macrophthalmus* Bloch, 1792 by subsequent designation of Cuvier, 1829 (= *Sciaena hamrur* Forsskål, 1775)].

*Boops* Gronovius, 1854: 58 (type species, *Boops asper* Gronovius, 1854, by monotypy) (preoccupied by *Boops* Cuvier, 1815, a genus of Sparidae).

**Diagnosis.** — Circumtropical genus of Priacanthidae containing majority of members of family with maximum sizes of species ranging from perhaps under 200 to little over 300 mm SL. Adults moderately elongate-ovate, laterally compressed; juveniles more deep-bodied. Anterior profile usually asymmetrical, tip of lower jaw being above or below midline of body. Possible sexual dimorphism in fin lengths noted in one species. The following morphological conditions which vary within Priacanthidae serve to distinguish *Priacanthus*. Scales relatively small, 56–115 in lateral series. Scales of head region less modified than those of *Pristigenys* (Fig. 1) or *Cookeolus*, with spinules less prominent, but more so than *Heteropriacanthus*; scales more exposed than in the latter genus resulting in rougher texture. Scales present on preopercle posterior to shelf overlying sensory canal. Branchiostegal rays 1–4 with few scales present. Scales of midlateral surface of body with posterior (apical) field elevated, overlying a separate well developed flange which is contiguous with dermis (Fig. 3a); apical field broadly pointed, of varied length, with spinules along posterior margin and surface with total spinules ranging from fewer than 20 in juveniles of some species to 100 or more in adults of some species (Figs. 2e, f, 3b, d, e–g); two species with apical field reduced to narrow or pointed flange (Fig. 3c, h) on scales of adults. Anterior margin of lateral body scales with three or four interradiat projections; scale circuli essentially smooth ridges (Fig. 4d). Spinous portion of dorsal fin of graduated height, tenth spine longest. Soft portions of dorsal and anal fins with 11–15 and 12–16 rays respectively, moderately long, ranging from subequal to about 1.5 times eye diameter, rounded to pointed. Caudal fin rounded, truncate, crescentic, or lunate. Pelvic fins of moderate length, usually reaching to or well beyond anal-fin origin. Spinules variable on dorsal spines, developed on anal and pelvic spines; spinules present on basal four-fifths of soft dorsal, anal and pelvic rays, basal one-half of pectoral rays. Shelf overlying sensory canal of preopercle little pronounced, smooth margined, except occasionally serrate over spine base; canal relatively closed with small elongate openings; preopercular spine finely serrate, well developed to obsolescent in adults. Interopercle notched posteriorly (often overlain by very thin sheet of bone in *P. fitchi*). Nasal bones spatulate, lacking serrations on anterior shaft. Lacrymal, second infraorbital (and 3 in some species) with coarse serrations and spines or fine serrations only (Fig. 5a). Gill rakers on first arch 17–32. Pseudobranchs with about 55–90 filaments. Teeth on dentary about 25–45, vomer 25–65, palatine 25–40, premaxilla 70–110. Anterior and posterior ceratohyals joined by a broad suture (Fig. 5d). Frontal bones meeting medially in a sagittal crest. Bones overlying saccular regions of skull much modified to form deep fossae

which receive anterior extensions of swimbladder (Fig. 6b). Accessory neural arch incomplete as in *Heteropriacanthus* (Fig. 7c). Posterior pleural ribs with narrow flanges (Fig. 5f). Epipleurals present on ribs of vertebrae 3–7. First haemal spine massive, elongate, interdigitating with and bound to basal anal pterygiophores (Fig. 8b). Posterior zygapophyses of caudal vertebrae fused to haemal spines to form lateral foramina (Fig. 8b). Procurent caudal rays 5+5. Predorsal bone lacking. Supracleithrum essentially as in *Pristigenys* (Fig. 5g). Pelvic bones with a large ventral keel as in *Cookeolus* (Fig. 5e); postpelvic processes narrow, not expanded distally (Fig. 5c). Swimbladder with anterior and posterior projections (Fig. 9c), the anterior associated with saccular fossae of skull. Extrinsic swimbladder muscles present, originating on first pleural rib and inserting on anterior portion of bladder either ventrolaterally or ventromedially (Fig. 10b, c). Pyloric caecae of moderate length, length 4–6 times thickness, about 11–13 in number. Gonads broadly triangular, especially in gravid females.

*Remarks.*—Jordan (1919), Neave (1939), Golvan (1962), and possibly others list “*Bogata*” Blyth (1860) as a synonym of *Priacanthus* and/or a valid nominal genus of fish. However, inspection of Blyth’s work reveals these listings to be misspellings of *Bogada* Bleeker (= *Chanda*, a genus of ambassid, according to recent authors) based on Blyth’s description of a new species, “*Bogada infuscata*”, from the Sitang River, Burma. The description proposes no new generic name and clearly indicates an ambassid or similar secondary freshwater fish for the nominal *infuscata*, not a juvenile *Priacanthus* as construed by Jordan (1919). The name “*Bogata*” Blyth is thus not available.

### *Priacanthus alalaua* Jordan and Evermann

Plate IIIb; Figure 3a, b

*Priacanthus alalaua* Jordan and Evermann, 1904: 181 (Honolulu, Hawaiian Is.).

*Diagnosis.*—A relatively large (to perhaps 275 mm SL in E Pacific) to relatively small (less than 200 mm SL in Hawaiian Is.) member of *Priacanthus hamrur-blochii* species group defined by reduced or obsolescent preopercular spine in adults and black basal spot on pelvic fins. A member of the *blochii* subgroup (including also *nasca* and *sagittarius*) characterized by thicker, less tapered gill rakers (Fig. 18a) and reduced gill raker counts (fewer than 23). Distinguished from *P. blochii* and *P. sagittarius* by much longer pectoral fins (1.3–1.6 in head length vs. 1.9–2.2). Distinguished from *P. nasca* by lower scales counts (LS = 72–84 vs. 89–94).

*Description.*—Based on 20 specimens, dorsal-fin rays X, 13 (12–14); anal-fin rays III, 14 (13–14); pectoral-fin rays 18 (17–19). Scales in lateral series 72–84 (80.0); lateral-line scales 65–79 (71.2); vertical scale rows 53–58 (55.7), 10–13 above lateral-line, 40–45 below. Total gill rakers on first arch 19–23 (20.5), 14–18 on lower limb, 4–6 on upper.

General profile evident in Plate IIIb. Largest specimen examined 260 mm SL (E Pacific); largest Hawaiian specimen examined 190 mm SL. Caudal fin truncate. Soft portions of dorsal and anal fins broadly rounded and of moderate length, subequal to eye diameter. Pectoral fins relatively long and pointed, subequal or exceeding length of pelvic spines. Pelvic fins reaching first anal-fin spine. Preopercular spine obsolescent in specimens over 100 mm SL, reduced to a small

triangular prominence scarcely projecting beyond preopercular margin. Lacrymal and second infraorbital with fine serrations as in *P. sagittarius* (Fig. 5a). Midlateral scales (Fig. 3a, b) somewhat constricted medially, with expansive spine-bearing apical field (about one-half area of anterior field), broadly pointed posteriorly, with about 40–60 spinules on surface and posterior margin. Extrinsic swimbladder muscles as in *P. hamrur* (Fig. 10b).

Body proportions are based on 20 specimens 101–260 mm SL. BD 367–435 (398), BW 139–181 (160), CPL 126–153 (139), CPD 072–089 (082), HL 305–387 (340), HD 336–409 (351), HW 159–258 (199), ORB 138–206 (162), IO 079–098 (088), SN 085–115 (098), JW 178–230 (201), D1L 119–168 (145), D2L 151–212 (177), AL 121–199 (161), PIL 196–225 (210), P2L 253–317 (287). Ontogenetic variation is evident in several morphometric distances, especially soft dorsal and pelvic fins which become proportionately longer with maturity. There is slight negative allometry in body width. The two largest specimens remain laterally compressed and do not show the abrupt increases in girth of several other *Priacanthus* species. There is also slight negative allometry in head width and length and snout length.

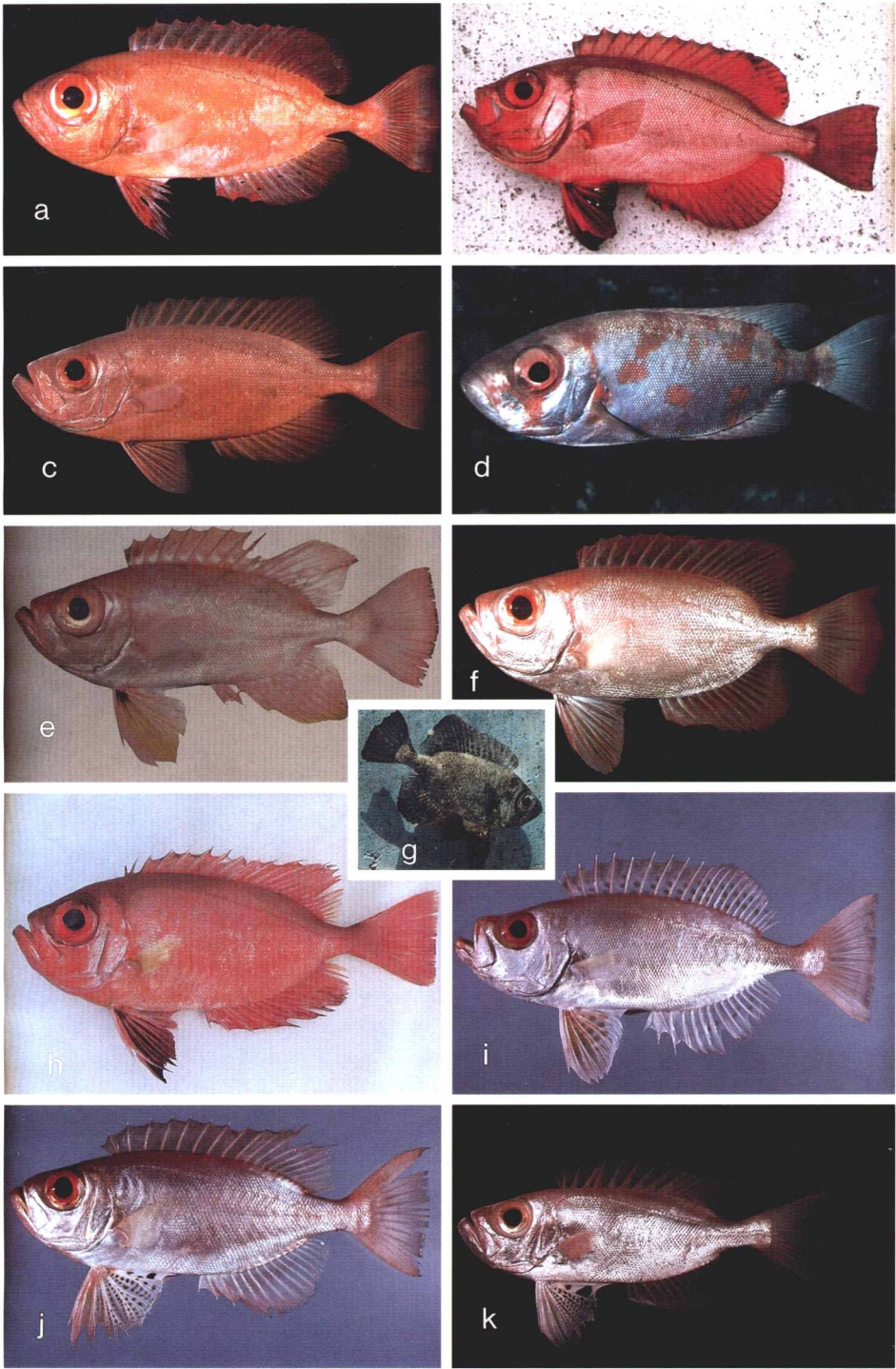
Color in life (based on color photo), crimson on head, iris of eye, body and fins. Membranes of dorsal, anal and caudal fins light dusky, darker near margins. Pectoral fins clear or pink. Pelvic fin membranes black, especially on distal three-quarters, with a more intense black blotch basally on dorsal surface. Pigmentation of pelagic juveniles is not known.

*Distribution.*—Recorded from Hawaiian Islands and eastern Pacific off Baja California and in the Revillagigedo Islands (Fig. 19); questionably occurs more widely in eastern Pacific.

*Geographic Variation.*—There is great disparity in maximum sizes of specimens examined from the eastern Pacific and Hawaiian Islands possibly resulting from a rather unlikely collecting artifact or from dwarfism in Hawaiian populations. Gosline and Brock (1960) gave a length “to 14 inches” for *alalaua* but they apparently lacked a clear impression of this species as they suggested the possibility of its being a synonym of *P. hamrur*. The latter is not similar to *alalaua* and is, in fact, very similar to another Hawaiian species, *P. meeki*, which attains large size. Of over 200 Hawaiian specimens examined, including many R/V TOWNSEND CROMWELL trawl specimens recently received at SOSC but not listed in Material Examined, the largest is BPBM 10877 at 190 mm SL. Several eastern Pacific specimens are much larger (to 260 mm SL). In spite of this enigma, significant differences in either meristic data or shape between these populations are not apparent.

→

Plate III. a) *Priacanthus nasca*, holotype, 268 mm SL (BPBM 30544), Easter Island, photo J. E. Randall; b) *Priacanthus alalaua*, about 215 mm SL, Revillagigedo Islands, photo L. Stockland; c) *Priacanthus blochii*, 155 mm SL, Samoa, photo J. E. Randall; d) *Priacanthus blochii*, about 200 mm SL, Bali, photo J. E. Randall; e) *Priacanthus sagittarius*, 193 mm SL (USNM 236936), Samoa, photo R. Wass; f) *Priacanthus sagittarius*, 205 mm SL, Ambon Island, photo J. E. Randall; g) *Priacanthus sagittarius*, 252 mm SL (HUJ F.11152), Gulf of Aqaba, photo A. Diamant; h) *Priacanthus zaiserae*, 165 mm SL, Japan, photo H. Masuda; i) *Priacanthus macracanthus*, 187 mm SL, Western Australia, photo G. Leyland; j) *Priacanthus tayenus*, 187 mm SL, Western Australia, photo G. Leyland; k) *Priacanthus tayenus*, 151 mm SL, Philippine Islands, photo J. E. Randall.



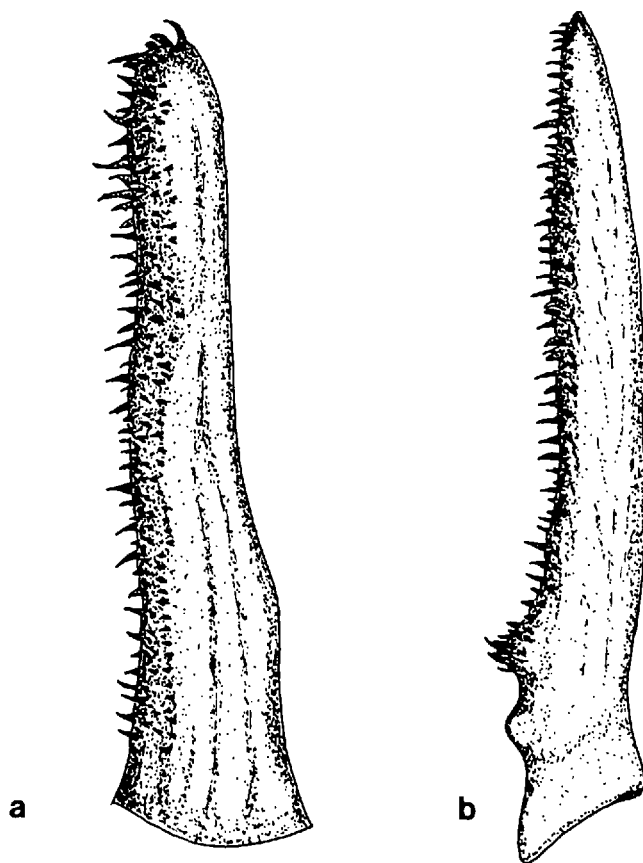


Figure 18. Gill raker forms of: a) *Priacanthus sagittarius*, b) *Priacanthus hamrur*.

*Biological Notes.*—Occurs mostly at depths of 100 m or more to at least 275 m in Hawaii and has been captured at night in eastern Pacific localities at relatively shallow depths (9–46 m) (Fitch and Crooke, 1984). Inhabits rocky bottoms but many specimens have been trawled from relatively open bottom in Hawaiian waters. Gonads of specimens collected in Hawaii in November appear to be nearing spawning condition.

*Remarks.*—The systematic implications of the possible dwarfism discussed above in Hawaiian populations of *P. alalaua* are not understood. If a reality, the phenomenon may be ecophenotypic in nature or genetic. If the latter is the case, then genetic isolation from eastern Pacific populations must be nearly or wholly in effect. However, the lack of any corroborative variation in other morphological characters seemingly precludes any taxonomic recognition of these populations above a racial level. Unfortunately, Rosenblatt and Waples (1986) lacked Hawaiian *alalaua* material to include in their comparative biochemical studies of proteins in fishes of these regions which might have shed more light on the problem.

Fowler (1928) and Tinker (1944, 1978) incorrectly synonymized this species with *P. hamrur* resulting in spurious Hawaiian records for that species. Von Bonde (1923) reports *alalaua* from South Africa, probably based on *P. hamrur*.

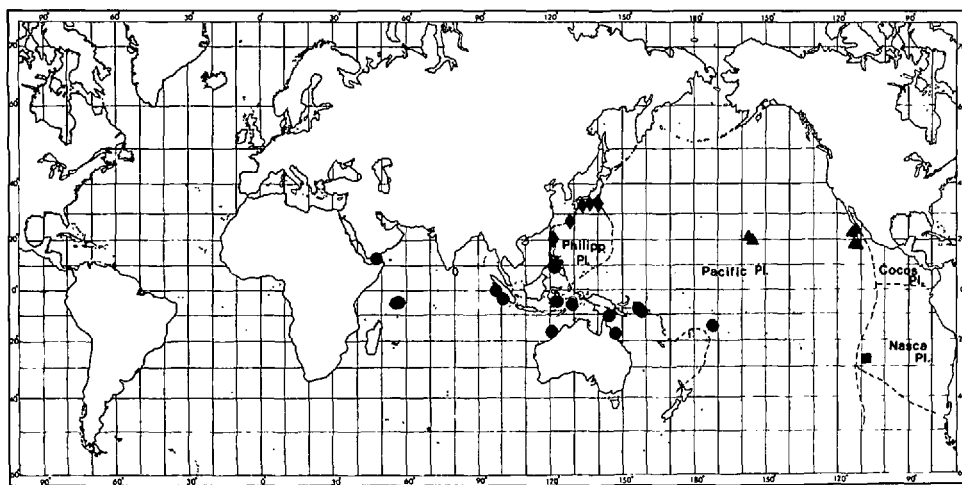


Figure 19. Distributions of *Priacanthus blochii* (circles), *P. zaiserae* (diamonds), *P. alalaua* (triangles), *P. nasca* (square).

**Material Examined.**—77 specimens, 64–260 mm SL. HAWAIIAN ISLANDS: BPBM 10877,1; BPBM 22430,4; BPBM 23669,1; BPBM 23721,1; BPBM 23923,1; BPBM 23974,4; BPBM 24724,1; BPBM 24834,11; BPBM 25080,4; BPBM 25879,2; BPBM 26401,1; FMNH 21502,1; LACM 308,1; LACM 32242-30,23; LACM 32668-33,3; SU 7461,1 (paratype); USNM 50643,1: 170 mm SL (holotype); USNM 125659,1 (paratype); USNM 282887, 7; USNM 55099,1. MEXICO: LACM 38336-1,1; LACM 39584-1,1; USNM 167567,1; REVILLAGIGEDOS ISLANDS: LACM 38338-1,2; LACM 38340-2,2; LACM 43774-11,1.

*Priacanthus arenatus* Cuvier  
Plate IIc; Figure 6b

*Priacanthus arenatus* Cuvier, 1829: 101 (Brazil).  
*Priacanthus insularum* Johnson, 1862: 179 (Madeira).  
*Priacanthus catalufa* Poey, 1864: 177 (Cuba).

**Diagnosis.**—A relatively large (to perhaps 370 mm SL) member of *Priacanthus hamrur-blochii* species group defined by an obsolescent preopercle spine in adults and black basal spot on pelvic fins. A member of the *hamrur* subgroup (including also *meeki* and *prolixus*) distinguished from members of *blochii* subgroup and *P. zaiserae* by having a crescentic caudal fin and increased soft dorsal- and anal-fin ray counts (modally 14 & 15 vs. 13 & 14). Distinguished from *P. hamrur* of the Indo-Pacific by higher gill raker counts ( $\bar{x}$  = 29.8 vs. 25.5, 6–8 vs. 4–6 on upper limb). Distinguished from *P. meeki* of Hawaiian Islands by lower scale counts (LS 83–91 vs. 104–115).

**Description.**—Based on 30 specimens, dorsal-fin rays X (rarely XI), 14 (13–15); anal-fin rays III, 15 (14–16); pectoral-fin rays 18 (17–19). Scales in lateral series 83–91 (86.3); lateral-line scales 71–84 (76.5); vertical scale rows 49–59 (53.4), 10–14 above lateral-line, 38–45 below. Total gill rakers on first arch 28–32 (29.8), 21–24 on lower limb, 6–8 on upper.

General profile evident in Plate IIc. Largest specimen examined 362 mm SL. Caudal fin crescentic. Soft portions of dorsal and anal fins broadly rounded, of



moderate length, subequal or slightly exceeding eye diameter. Pectoral fins relatively short and broadly pointed, shorter than pelvic spines. Pelvic fins usually reaching to third anal spine. Preopercular spine reduced to a slight prominence in larger adults. Lacrymal and second infraorbital with fine serrations as in *P. sagittarius* (Fig. 5a). Extrinsic swimbladder muscles situated as in *P. hamrur* (Fig. 10b). Midlateral scales as described for *P. meeki* (Fig. 3f).

Body proportions are based on 28 specimens 111–230 mm SL. BD 320–403 (362), BW 127–174 (154), CPL 128–161 (146), CPD 068–122 (079), HL 280–346 (315), HD 284–346 (318), HW 159–249 (180), ORB 124–170 (144), IO 066–088 (076), SN 079–100 (092), JW 172–210 (191), D1L 123–159 (141), D2L 099–195 (155), AL 094–175 (140), P1L 156–194 (176), P2L 219–323 (281). Notable ontogenetic variation is apparent in only two distance measurements, orbit diameter and lower jaw length, both of which exhibit negative allometry. A number of other characters are quite variable, especially in younger specimens, but show no definite ontogenetic patterns.

Color in life (based on per. obsv. and illustrations) bright red or pink on head, iris of eye, body and fins with silvery blotches sometimes apparent. About 15 dark red spots sometimes evident along lateral line. Dorsal-, anal- and caudal-fin membranes with light dusting of melanophores, darker near fringes. Pectoral fins clear or slightly pink; pelvic fin membranes dusky, darkest on distal two-thirds, with a black basal spot on dorsal surface. It is possible that *arenatus* may at times exhibit the silvery-white and red barred color phase or fin spotting described for the closely related *hamrur* but evidence of these has not been observed by the author.

Pelagic juvenile specimens available (30–35 mm SL) are from scombroid stomachs and pigmentation is deteriorated. However there is evidence of three dark bands or rows of dark spots in the spinous dorsal fin. The soft portions of the dorsal and anal fins seem to be blotched anteriorly with the posterior seven to eight interradiial membranes clear or whitish; there are remnants of dark bands on the caudal fin and the pelvic fins are heavily pigmented with melanophores on distal two-thirds. The body is probably silvery to dusky in life, as in pelagic stages of other species; there is no evidence of dark blotching on the body or head.

*Distribution.*—Tropical and tropically influenced areas of the western and eastern Atlantic Ocean in both insular and continental waters (Fig. 20). In western Atlantic, adults occur north to at least North Carolina and Bermuda; juveniles are commonly carried northward by the Gulf Stream to New York (Latham, 1916; Foehrenbach, 1968) and occasionally to Nova Scotia (MacKay and Gilhen, 1973). In eastern Atlantic from Madeira (Johnson, 1862) to northern Angola (Poll, 1954). Erroneously reported from the Indo-Pacific by some authors (Fowler, 1931; Smith, 1949).

*Geographic Variation.*—Despite the possible allopatry of eastern and western Atlantic populations of *P. arenatus*, regional variation is not great. The only significant meristic difference is in vertical scale rows, which averages higher in western Atlantic specimens (55.1 vs. 51.5). Morphometrically, young specimens from the eastern Atlantic have shorter average soft dorsal and anal fins and body depths than western Atlantic specimens. There are, however, overlaps within this size range and adults from both regions are totally overlapping in these characters.

*Biological Notes.*—Recorded from depths less than 20 m to over 200 m near reefs, patch reefs and apparently, at times, more open sandy bottom areas where it is commonly trawled. Loose aggregations of adults occur over patch reef areas and



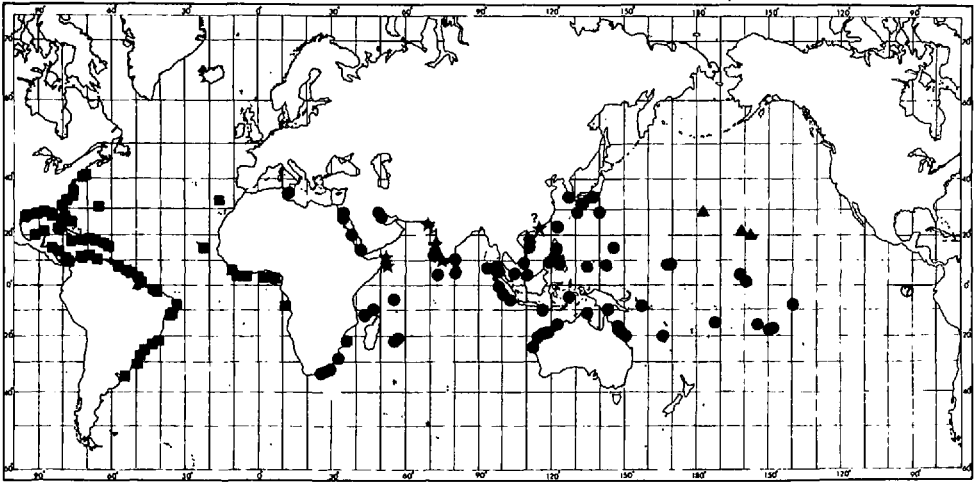


Figure 20. Distributions of members of *Priacanthus hamrur* species subgroup: *P. arenatus* (squares), *P. hamrur* (circles) (asterisk denotes probable Suez migrant), *P. meeki* (triangles), *P. prolixus* (stars), possible undescribed form from Galapagos (circled question mark).

spacing of these fishes may indicate territoriality (Shipp and Hopkins, 1978). In those island habitats where it is syntopic with *Heteropriacanthus cruentatus*, *P. arenatus* usually occurs at depths over 20 m while *cruentatus* inhabits shallower waters (Longley and Hildebrand, 1941). Caldwell and Bullis (1971) reported tremendous aggregations of pelagic juveniles (30–40 mm SL) in shallow waters in the West Indies during the month of February and similar-sized specimens have been removed from stomachs of mackerel captured in April. Gonads of larger females collected in September from the Caribbean and off Surinam appeared to be very near spawning condition.

*Remarks.*—The biregional distribution suggested by Figure 20 for *P. arenatus* raises questions concerning the possible allopatry of these populations and the taxonomic implications of such a distribution. However, the relatively minor interregional variation described above would suggest that these populations maintain genetic communication, albeit possibly restricted. This communication is probably facilitated by occasional transport of pelagic juveniles from the Caribbean region to the eastern Atlantic via the eastern effluent of the Gulf Stream and, conversely, westward by the Equatorial currents.

*P. arenatus* is highly similar to *P. hamrur* and *P. prolixus* of the Indo-Pacific and *P. meeki* of the Hawaiian Pacific region, differing from them appreciably only in meristics or morphometry (see "Diagnosis"). *Priacanthus arenatus* may, in addition, be overall more plainly pigmented than *hamrur* which, in some specimens, has the median fins virtually black or, alternately, with dusky spots. Though often somewhat dusky, no evidence of such contrasting dark pigmentation has been observed in available material of *arenatus* or *meeki*. Caldwell (1962a) stated that *arenatus* might in fact be synonymous with Indo-Pacific forms, but the consistent meristic differences shown herein and the apparent allopatry of these populations suggest these are distinct species. See "Remarks" of *P. meeki* account regarding possible undescribed species which may key to *arenatus* herein.

The type specimens of *Priacanthus insularum* Johnson (1862) and *P. catalufa* Poey (1864) are apparently no longer extant but the original descriptions are clearly referable to *P. arenatus* based on caudal fin shape and several other characters. See comments under *Heteropriacanthus cruentatus* regarding the nomenclatural status of *Priacanthus fulgens* Lowe (1838).

*Material Examined.*—198 specimens, 30–362 mm SL. ALABAMA: USNM 155540,1. BAHAMAS: AMNH 28368,1; USNM 171001,1; USNM 38449,2. BRAZIL: CAS 18516,1; CAS 42947,2; CAS 59271,3; CAS 59272,2; CAS 59275,1; CAS 59276,1; CAS 59277,1; CAS 59284,1; LACM 3039,3; LACM 3041,1; MNHN A.3066,1: 55 mm SL (syntype); MZUSP 13333,1; MZUSP 13334,1; MZUSP 2381,1; MZUSP UNCAT.,1; MZUSP UNCAT.,1; MZUSP UNCAT.,1; SU 59273,1; USNM 104312,1; USNM 156848,1; USNM 159816,1; USNM 23225,1; USNM 282886,2; USNM 82865,1. CAPE VERDE ISLANDS: MNHN 41-30,3. COLOMBIA: LACM 9217-4,1; USNM 282888,3. CUBA: USNM 24777,1; USNM 110728,1 (skel); USNM 110729,1 (skel); USNM 110730,1 (skel); USNM 282928,1 (skel); USNM 282930,1 (skel); USNM 37520,2. DOMINICAN REPUBLIC: LACM 6879-1,2. FLORIDA: AMNH 4567,1; CAS 32589,1; LACM 9209-1,1; USNM 117071,5; USNM 117072,1; USNM 127148,1; USNM 155541,1; USNM 187979,2; USNM 204949,2; USNM 204951,1; USNM 282942,1 C&S. FRENCH GUIANA: LACM 3038,1; LACM 3115,1; CAS 48794,1; USNM 282854,3. GEORGIA: USNM 282884,1; USNM 282893,3 C&S. GULF GUINEA: BMNH 1930.8.26:29,2; BMNH UNCAT.,2; MNHN 1967-816,1; MNHN 1971-82,3; UMML 15857,3; UMML 16332,2; UMML 16596,3; UMML 16797,1; UMML 21370,1; UMML 21394,1; UMML 21412,2. GULF MEXICO: CAS 49845,2; CAS 63263,2. GUYANA: USNM 159811,3; USNM 159817,2; USNM 159828,1; USNM 159831,6; USNM 159891,1; USNM 282853,1. HAITI: USNM 133710,1. HONDURAS: LACM 30737-5,1. JAMAICA: SU 11789,1. LESSER ANTILLES: AMNH 30412,1; USNM 183568,9. LIBERIA: MNHN 62-272,2; USNM 193708,1. LOUISIANA: USNM 179726,1; USNM 155547,1. MASSACHUSETTS: USNM 16943,2; USNM 20630,1; USNM 20680,1; USNM 22091,1. MEXICO: LACM 2353,1; USNM 186459,1; USNM 187085,1; USNM 187977,1; USNM 192366,1. NEW YORK: AMNH 12518,1; AMNH 15340,1; AMNH 50934,2. NICARAGUA: USNM 187978,1. NORTH CAROLINA: AMNH 50464,2; 50467,1; LACM 8810-1,2; UF 27698,1; USNM 152051,1; USNM 152074,1. PANAMA: USNM 81930,2. PUERTO RICO: AMNH 26282,1; CAS IU 9423,1; LACM 9207-1,2; SU 11788,1; SU 12647,1; SU 8265,1; USNM 187980,1; USNM 50138,1. RHODE ISLAND: USNM 20729,1; USNM 20730,1; USNM 20731,3. SIERRA LEONE: USNM 282926,1. SOUTH AMERICA?: MNHN A.3085,1: 96 mm SL (syntype). SOUTH CAROLINA: 152075,1; 204952,1; 204953,1. SURINAME: CAS 48453,2; USNM 185250,2; USNM 185310,1; USNM 185312,1; USNM 185375,1; USNM 186175,1. TEXAS: USNM 159893,1; USNM 185347,1; USNM 186473,3 (1 C&S). VENEZUELA: LACM 7626,1; LACM 7627,2; LACM 9210-1,3; USNM 282855,2. VIRGINIA: USNM 90885,1; USNM 196853,1.

*Priacanthus blochii* Bleeker  
Plates IIIc, d; Figure 2e

*Priacanthus blochii* Bleeker, 1853: 456 (Indonesia).

*Diagnosis.*—A medium-sized (to perhaps 250 mm SL) member of *Priacanthus hamrur-blochii* species group defined by a reduced or obsolescent preopercular spine in adults and black basal spot on pelvic fins. A member of the *blochii* subgroup (with *alalaua*, *nasca*, *sagittarius*) characterized by thicker, less tapering gill rakers (Fig. 18a) and reduced gill raker counts (fewer than 23). Distinguished from *P. alalaua* by much shorter pectoral fins (1.9–2.2 in head length vs. 1.3–1.6), by longer upper jaw (goes much less than twice in head length vs. about twice), and by morphology of adult scales (Figs. 2e, 3b). Distinguished from *P. nasca* by same pectoral fin and scale morphology characters and by lower scale counts (74–85 vs. 89–94). Distinguished from *P. sagittarius* by lacking black blotches in first two spinous dorsal membranes, relatively low and round soft dorsal and anal fins (vs. longer and more angulate), higher scale counts (74–85 vs. 67–74), and morphology of adult scales (Figs. 2e, 3h).

*Description.*—Based on 30 specimens, dorsal-fin rays X,13 (12–14); anal-fin rays III,14 (13–15); pectoral-fin rays 17 (17–19). Scales in lateral series 74–85 (78.5);

lateral-line scales 69–77 (71.4); vertical scale rows 47–56 (50.4), 8–13 above lateral-line, 36–43 below. Total gill rakers on first arch 17–22 (20.2), 14–17 on lower limb, 3–5 on upper.

General profile evident in Plate IIIc. Largest specimen examined 235 mm SL. Caudal fin rounded. Soft portions of dorsal and anal fins broadly rounded, relatively long, about 1.2 times eye diameter. Pectoral fins relatively short, broadly pointed, shorter than pelvic spine length. Pelvic fins usually reaching to or beyond anal fin origin. Preopercular spine reduced in adults, not quite reaching posterior tip of interopercle. Lacrymal and second infraorbital with fine serrations as in *P. sagittarius* (Fig. 5a). Extrinsic swimbladder muscles situated as in *P. hamrur* (Fig. 10b). Midlateral scales with expansive apical field bearing 70–90 spinules on surface and posterior margin at full development (Fig. 2e).

Body proportions are based on 25 specimens 128–235 mm SL. BD 340–383 (360), BW 144–173 (161), CPL 125–149 (139), CPD 080–092 (087), HL 300–343 (318), HD 286–368 (318), HW 166–196 (180), ORB 129–167 (146), IO 069–084 (076), SN 085–102 (093), JW 191–215 (202), D1L 123–170 (140), D2L 160–208 (179), AL 163–208 (183), P1L 152–191 (169), P2L 277–321 (302). There is slight positive allometry in caudal peduncle depth, length of soft portions of dorsal and anal fins, and width of head and body. Negative allometry is apparent in interorbital distance and length of lower jaw.

Color in life (based on transparencies) bright red on head, iris of eye, body and fins, or, alternately, silvery white on head and body blotched with red (Plate IIId). Specimens photographed underwater at widely separated localities exhibited blotches in approximate same positions. About 15 dark red spots sometimes evident along lateral-line. Membranes of dorsal, anal and caudal fins lightly dusted with melanophores, darker near fringes. Pectoral fins clear or pink; pelvic fin membranes light dusky to dark, especially distally, with a black spot basally on dorsal surface. Gill rakers red (T. Gloerfelt-Tarp, in litt.). Pelagic juvenile pigmentation unknown.

*Distribution.*—In Indo-Pacific, apparently along an equatorial axis, being recorded from Gulf of Aden to Samoa and north to Philippines and south to northern Great Barrier Reef of Australia. Not recorded from Pacific Plate except at Samoa. Lee's (1980) records from Taiwan are erroneously based on the form herein described as *P. sagittarius*. Shen's (1984, fig. 303-4) purported illustration of *P. blochii* from Taiwan appears to represent *Heteropriacanthus cruentatus*.

*Geographic Variation.*—Based on relatively small regional samples, east-west clinal variation in some meristic characters is evident in *P. blochii*. Scale counts and pectoral-fin rays increase in an easterly progression—western Indian Ocean mean LS = 75.3, P<sub>1</sub> = 17.1; Indonesia-Philippines 80.3, 17.5; southwestern Pacific (Australia and New Guinea to Samoa) 81.3, 18.0, with the two eastern-most specimens from Samoa being 84 and 85, 18 and 19. Other meristic and morphometric data do not show patterns of regional variation.

*Biological Notes.*—All specimens for which depth information is available have been taken in the 15–30 m range. *Priacanthus blochii* apparently prefers reef areas and is rarely trawled. Females collected from the Seychelles in March appeared to be nearing spawning based on condition of the gonads.

*Remarks.*—*Priacanthus blochii* Bleeker has been confounded over the years with the somewhat similar appearing and broadly allopatric *P. hamrur* and was synonymized therewith by Bleeker himself (1873a) and followed without scrutiny in

several regional works (Weber and de Beaufort, 1929; Herre, 1953 and others). However, this study has shown that these forms are quite distinct and probably not even intimately related (see "Phylogenetic Analysis").

Kyushin et al. (1977, 1982), Lee (1980, 1984), and possibly Shao and Chang (1985) ascribed the epithet *blochii* Bleeker to the form herein described as *P. sagittarius*. The types of *blochii* are putatively among a series of 13 specimens now deposited at Leiden (RMNH 5552) (M. J. P. van Oijen, in litt.). Five specimens fall within the syntypic size range given by Bleeker (165–364 mm) ranging from 165 to about 240 mm TL (remaining 8, not seen, are recat. RMNH 30585). It is assumed that the 364-mm specimen was lost or distributed elsewhere during the disposition of Bleeker's collection. It greatly exceeds the size range of all other *blochii* specimens examined and is probably referable to another species. The smallest of the five possible types is a specimen of *P. hamrur* (now recat. as RMNH 30589); the four remaining are all the form here regarded as *P. blochii*. Of the four, a 167 mm SL specimen is selected as lectotype (RMNH 5552) and three (162–ca. 200 mm SL) as paralectotypes (RMNH 30583). Most of Bleeker's description will not distinguish between *P. blochii* and *P. hamrur*, though his reference to a truncate caudal fin clearly suggests a description based primarily on the former; *hamrur* specimens within the syntypic size range would have a notably crescentic caudal fin. None of the specimens are referable to the form herein described as *sagittarius* and the ascriptions of Kyushin et al. (1977) and the others are therefore erroneous.

*Material Examined.*—36 specimens, 89–235 mm SL. GULF ADEN: BMNH uncat., 2. INDONESIA: BPBM 29939, 1; BPBM 30191, 2; RMNH 316, 2; RMNH 5552, 1; 167 mm SL (lectotype); RMNH 30583, 3 (paralectotypes); USNM 210036, 1; USNM 282943, 1 C&S. NEW GUINEA: AMNH 16564, 1. PHILIPPINES: USNM 183205, 1; USNM 282932, 2. QUEENSLAND: QM I.16027, 1. SAMOA: BPBM 17485, 1. SEYCHELLES: ANSP 108322, 3; ANSP 108323, 3; ANSP 108334, 1; ANSP 108335, 2; ANSP 108340, 1; ANSP 108425, 1; MSNVR 556, 1. SOLOMON ISLANDS: BPBM 17372, 3; CAS GVF 1812, 1. SUMATRA: MNHN A.167, 1. LOCALITY UNKNOWN: BMNH 1906.10.24:141.

### *Priacanthus fitchi* new species Starnes

Plate 1h; Figure 3e

*Holotype.*—USNM 263760, 149 mm, sex undetermined, Indonesia, off Sumatra, 00°25'S, 98°40'E, trawled 150 m, T. Gloerfelt-Tarp, 7 May 1983.

*Paratypes.*—AMS I.26843-001, 117 mm SL, Western Australia, off Browse Island, 13°45'S, 123°30'E, trawl 250 m, vessel UMITAKA MARU, 23 December 1969; BMNH 1987.6.1:5, 103 mm SL, same data as AMS I.26843-001; BPBM 31881, 101 mm SL, same data as AMS I.26843-001; CAS 60361, 130 mm SL, same data as AMS I.26843-001; MNHN 1987-936, 131 mm SL, same data as AMS I.26843-001; USNM 183207, 117 mm SL, Philippines, Ponson Island, R/V ALBATROSS, 17 March 1909; USNM 284044, 124 mm SL, Indonesia, south of Sumatra, 01°25'S, 100°19'E, trawl 225–236 m, T. Gloerfelt-Tarp, 5 December 1983; USNM 285181, 2:94–126 mm SL (1 C&S), same data as AMS I.26843-001; WAM P.25394-003, 88 mm SL, Western Australia, Rowley Shoals, trawl 317 m, vessel UMITAKA MARU, 20 December 1969; WAM P.25399-012, 7:69–185 mm SL, same data as AMS I.26843-001; WAM P.26291-007, 3:95–105 mm SL, Indian Ocean, 17°33'S, 119°43'E, trawl 290–293 m, K. Sainsbury et al., 10 June 1978.

*Diagnosis.*—An apparently small (to perhaps less than 200 mm SL) *Priacanthus* distinguished from members of *hamrur-blochii* species group by usually having a well developed preopercular spine at all sizes and lacking a black basal spot on dorsal surfaces of pelvic fins. Distinguished from *P. tayenus* by lacking inky black spots in pelvic fin membranes, having rounded (vs. more pointed) soft portions of dorsal and anal fins, and higher scale counts (LS = 77–87 vs. 56–73). Distinguished from the phenetically more similar *P. macracanthus* in lack of spots in fin membranes, having creamy white soft dorsal and anal fins, a slimmer, more tapered body, and, on the average, larger eye (ORB 157 vs. 143).

*Description.*—Based on holotype and 14 paratypes, dorsal-fin rays X, 13; anal fin III, 14 (13–14); pectoral-fin rays 18 (18–19). Scales in lateral series 77–87 (83.0); lateral-line scales 74–79 (76.3); vertical scale rows 45–51 (48.2), 8–10 above lateral-line, 36–41 below. Total gill rakers on first arch 22–25 (23.6), 18–20 on lower limb, 4–5 on upper.

General profile evident in Plate 1h. Largest specimen examined 185 mm SL. Body tapering considerably from behind head to beneath middle of soft dorsal fin in most, but not all specimens. Caudal fin truncate or very slightly concave. Soft portions of dorsal and anal fins broadly rounded, of moderate length, subequal to eye diameter. Pectoral fins relatively long and pointed, usually exceeding length of pelvic spines. Pelvic fins not reaching first anal spine except in largest specimen. Preopercular spine variable but well developed at all sizes, reaching to tip of subopercle or not. Interopercle variable posteriorly with notch often, but not always, overlain by thin sheet of bone. Lacrymal and second infraorbital with fine serrations as in *P. sagittarius* (Fig. 5a). Midlateral scales with expansive apical field bearing about 95–115 or more spinules at maximum development (Fig. 3e). Extrinsic swimbladder muscles essentially as in *P. hamrur* (Fig. 10b).

Body proportions are based on 15 specimens 88–185 mm SL. BD 286–350 (318), BW 112–143 (129), CPL 125–161 (143), CPD 063–076 (067), HL 295–352 (322), HD 265–331 (294), HW 164–188 (178), ORB 136–171 (157), IO 065–085 (072), SN 075–088 (082), JW 172–204 (188), D1L 113–143 (127), D2L 116–169 (142), AL 095–153 (130), P1L 195–245 (224), P2L 231–283 (262). Ontogenetic variation is evident only in distances reflecting dimensions of head, which appears disproportionately large in most specimens due to the tapered body configuration; both head depth and width are positively allometric.

Color in life (based on transparencies and published plates) silvery red or pink on head and body; iris of eye red. Fins creamy pink without evidence of spots. Posterior six to eight interradial membranes of soft portions of dorsal and anal fins conspicuously creamy white; interradial membranes of spinous portion of dorsal fin and anterior six to eight membranes of soft portions of dorsal and anal fins lightly dusted with melanophores. Pelvic fin membranes dusky. Pigmentation of pelagic juveniles is not known.

*Distribution.*—Presently known from eastern Indian and western Pacific Oceans (Fig. 21) from northwestern Australia, western Indonesia, the Philippines, and southern Japan (based on Okamura, 1985); possibly restricted to portions of the Indian-Australian and Eurasian tectonic plate regions.

*Biological Notes.*—A deeper water species trawled from relatively open bottom areas at depths of 150 to over 400 m and thought to be much more common at depths over 400 m, particularly along the margin of the northwestern shelf of Australia (G. Leyland, in litt.). Specimens taken at these depths range from less than 70 to 185 mm SL and all but one are less than 150 mm SL. Maximum size is not known but the species may be relatively diminutive based on material examined thus far. Specimens as small as 130 mm SL, collected in December, have ripe gonads, thus appearing sexually mature. The largest specimen examined (185 mm SL) appears to be a male nearing spawning condition.

*Remarks.*—*Priacanthus fitchi* and the sympatric Indo-Pacific species *P. macracanthus* are not distinguishable on meristic characters on an individual basis. Therefore it may be relatively difficult to assign preserved specimens which lack pigment and are less typical in body form (considerably tapered or not) to either taxon on an a posteriori basis. While gill rakers average lower in *fitchi* (23.6 vs. 25.0), coincidentally the lowest counts among *macracanthus* (low as 22) are from

within the Indonesian region of known sympatry of these species. However, a consensus of lower gill raker counts, pelvic fins usually falling well short of first anal spine, longer, more pointed pectoral fins (usually well over 20% of SL vs. less than 20%), and larger orbit (over 15% of SL vs. less than 15%) should favor a determination as *fitchi*. It is pointed out, however, that in the largest (185 mm SL) available specimen of *fitchi*, pelvic fins reach the first anal spine, so variation in this feature is not understood. In *macracanthus* the interopercle is usually notched posteriorly below the preopercular spine whereas in *fitchi* this notch is often covered by thin bone resulting in an entire posterior margin. Preopercular spines seem to consistently reach beyond the ventral tip of the subopercle in *macracanthus* but are variable in *fitchi*, often falling short. Fresh-caught specimens are, of course, easily separable on fin coloration.

This species is referred to as "Sp. 2" in Gloerfelt-Tarp and Kailola (1984) and Sainsbury et al. (1985); it is "sp. b" in Okamura (1985).

*Etymology.*—*fitchi* is a patronym for the late John E. Fitch, former ichthyologist with the California Department of Fish and Game, whom I never had the privilege of meeting, but with whom I exchanged much valuable information on priacanthid systematics prior to his death. His contributions to ichthyology, and especially to our knowledge of otolith morphology, are considerable.

### *Priacanthus hamrur* (Forsskål)

Plates IIe–h; Figures 4d, 9c, 10b, 18b

*Sciaena hamrur* Forsskål, 1775: 45 (Red Sea) (lectotype designated in Klausewitz and Neilsen, 1965).

*Anthias macrophthalmus* Bloch, 1792: 115 (Japan).

*Priacanthus speculum* Valenciennes, 1831: 471 (Seychelles).

*Priacanthus fax* Valenciennes, 1831: 473 (Seychelles).

*Priacanthus dubius* Temminck and Schlegel 1842: 19 (Japan).

*Boops asper* Gronovius, 1854: 58 (Indian Ocean).

*Priacanthus schlegelii* Hilgendorf, 1879: 79 (Japan).

*Priacanthus longipinnis* Borodin, 1932: 81 (New Caledonia).

*Diagnosis.*—A relatively large (to perhaps 300 mm SL) member of *Priacanthus hamrur-blochii* species group diagnosed by an obsolescent preopercular spine in adults and black basal spot on pelvic fins. A member of the *hamrur* subgroup (with *arenatus*, *meeki*, and *prolixus*) defined by a crescentic caudal fin and increased median fin-ray counts (usually 14 vs. 13 and 15 vs. 14 soft dorsal- and anal-fin rays respectively). Distinguished from very similar *P. arenatus* of the Atlantic by lower gill raker counts ( $\bar{x}$  = 25.5 vs 29.8, 4–6 vs. 6–8 on upper limb), from *P. meeki* of Hawaiian Islands by gill raker counts ( $\bar{x}$  = 31.4 in *meeki*) and lower scale counts (LS 79–96 vs. 104–115). Distinguished from partially sympatric *P. prolixus* by lower gill raker counts (24–26 vs. 29–31), higher vertical scale row counts ( $\bar{x}$  = 53.6 vs. 47.5), and greater body depth ( $\bar{x}$  = 379 vs. 326).

*Description.*—Based on 99 specimens, dorsal-fin rays X (rarely IX), 14 (13–15); anal-fin rays III, 14–15 (13–16); pectoral-fin rays 18–19 (17–20). Scales in lateral series 79–96 (87.4); lateral-line scales 70–90 (79.6); vertical scale rows 48–57 (53.6), 9–14 above lateral-line, 37–46 below. Total gill rakers on first arch 24–26 (25.5), 18–21 on lower limb, 4–6 on upper.

General profile evident in Plate IIe–h. Largest specimen examined 296 mm SL. Caudal fin crescentic, often emarginate in South African populations. Soft portions of dorsal and anal fins broadly rounded, moderately long, exceeding eye diameter. Pectoral fins relatively short and broadly pointed, shorter than pelvic spines. Pelvic

fins usually reaching to anal spines 2–3. Preopercular spine obsolescent in adults. Lacrymal and second infraorbital with fine serrations as in *P. sagittarius* (Fig. 5a). Midlateral scales as described for *P. meeki* (Fig. 2f). Extrinsic swimbladder muscles originating on first pleural rib and inserting anterolaterally on bladder (Fig. 10b).

Body proportions are based on 50 specimens 102–296 mm SL. BD 332–422 (379), BW 094–188 (156), CPL 134–159 (147), CPD 068–099 (086), HL 279–337 (310), HD 293–361 (326), HW 146–194 (172), ORB 113–160 (137), IO 063–093 (077), SN 076–133 (092), JW 171–210 (191), D1L 109–168 (143), D2L 143–205 (175), AL 109–207 (167), P1L 153–193 (173), P2L 260–322 (288). Ontogenic variation is apparent in a few distance measurements. Head length and depth, and lower jaw length all exhibit negative allometry relative to standard length and there are slight decreases in orbit diameter and length of spinous portion of dorsal fin with maturity.

Color in life (based on transparencies and published illustr.) bright red on head, iris of eye, body and fins, often blotched with silvery on freshly killed specimens. About 15 small dark spots sometimes evident along lateral line. Alternately (Pl. IIg), body may be silvery-white with 7 darker red bars (about two-thirds width of eye) of varied length on head and body, represented by faint dusky bars in preserved specimens. Bars are positioned beneath eye, before spinous dorsal fin, under dorsal spines 4–6, dorsal soft rays 3–5, posterior 3–4 soft rays, and on caudal peduncle. In this phase, top of head, premaxillae and prepelvic area may be reddish. Dorsal-, anal- and caudal-fin membranes light dusky to nearly black and darkest near margins or, in some specimens, dusky spots evident in dorsal and anal fin membranes which are reddish-brown in life (Pl. IIh). Pectoral fins clear to pinkish; pelvic fin membranes dusky to black on distal two-thirds, with dusky brown spots sometimes present; black blotch on dorsal surface of pelvic fins basally.

Juveniles (30 mm SL or so) pigmented essentially as described for *P. arenatus*. Three rows of dark spots (basal, medial, submarginal) on spinous portion of dorsal fin, centered on spines; basal row extending onto soft portion of dorsal fin to about third ray, remainder of fin clear or milky. First 4–5 anal fin membranes dusky; remainder of anal fin and caudal fin clear or milky; pelvic fin membranes dusky. Larger juvenile (44 mm SL) with dorsal, anal and distal one-half of caudal fins dark dusky with numerous light spots; pelvic fin membranes nearly uniform black.

*Distribution.*—Indo-Pacific region from Red Sea and southern Africa eastward to northern Australia and southern Japan and in central Pacific through Polynesia (Fig. 20). Abdelmoleh (1981) reports a specimen from Tunisia as a probable Suez Canal migrant but identity of specimen has not been confirmed. See *P. meeki* account for comments on questionable Galapagos Islands specimen. Hawaiian records reported by several authors (Fowler, 1928; 1931 and others) are based on misidentifications or misinterpretations of both *meeki* and *alalaua*.

*Geographic Variation.*—Regional variation in some meristic characters is apparent. Scale counts are high in Red Sea samples (LLS  $\bar{x}$  = 86.6), and low in Pacific Plate samples (76.0), but are comparable over the remainder of the Indo-Pacific, averaging near 80.0; no clinal trends are thus apparent. Many specimens from South Africa have a distinctly double emarginate caudal fin (Pl. IIh), compared to crescentic in all other populations, and are deeper bodied on the average ( $\bar{x}$  BD = 406 vs. about 380). Aside from these regional characteristics other attributes, such as pigmentation of fins (spotted vs. concolorous), do not seem to vary in any geographic pattern. It is not known if a given adult specimen may vary between

the two fin pigmentation conditions. Spotting of fins has been observed in specimens from South Africa, Somalia, northwestern Australia, Indonesia and Japan; uniformly colored fins have been observed from most of these regions as well. All specimens having spotted fins for which capture information is available were taken by trawling over more open bottom. Specimens from Somalia (USNM 290663) appear to be in spawning condition and fin spotting may be associated with open bottom habitats and/or reproductive condition.

*Biological Notes.*—Occurs primarily in reef areas at depths from less than 20 m to 250 m or more, but probably most common in 30–50 m range and preferring outer reef slopes (Amesbury and Myers, 1982); occasionally trawled from more open bottom areas (Senta, 1977; Wongratana, 1982). Examined heavily gravid females were collected during March in the Seychelles. The above mentioned specimens from Somalia, trawled away from reef areas during early May, may represent a spawning aggregation. Females as small as 160 mm SL appear to have ripe ovaries. Pelagic or recently settled juvenile specimens have been collected in April and May from western Pacific localities.

*Remarks.*—See “Remarks” under *Priacanthus prolixus* regarding status of that form and possible polymorphism in *P. hamrur*.

The type specimens of *Priacanthus dubius* Temminck and Schlegel (1842) and *Boops asper* Gronovius (1854) are apparently no longer extant. However, both names are referable to *P. hamrur* based on characters given in the original descriptions, particularly caudal fin shape. Curtiss (1938:95) introduced the name “*Priacanthus caroli*” into the literature in his treatise of Tahitian natural history. The name is referable to *P. hamrur* based on caudal fin description, fin-ray counts and other characters but should be considered invalid as it is only mentioned in passing, with no formal description, in the nonrefereed work.

*Material Examined.*—208 specimens, 30–296 mm SL. CAROLINE ISLANDS: BPBM 24602,2; CAS GVF 1445,1; CAS GVF 57-22,1; CAS GVF 75,1. COMORE ISLANDS: CAS 33133,1. INDIA: BMNH 1889.2.1:28,1; FMNH 91090,5; ROM 5432,1. INDONESIA: BPBM 19490,1; RMNH 30589,1; RMNH 314,1; SU 13787,1; USNM 183212,1; USNM 183233,6; USNM 183237,1; USNM 183238,1; USNM 263761,1; USNM 285019,1; USNM 285020,1; ZMA 116.110,1; ZMA 116.607,3; ZMA 116.608,2; ZMA 116.609,1. JAPAN: AMNH 26814,1; AMNH 26815,1; RMNH 315,1; SU 22816,4; UMMZ 176752,1; UMMZ 182790,1; USNM 151654,1; USNM 6436,2; USNM 71205,3; USNM 75473,1; ZMB 8156,1 ca. 235 mm SL (holotype of *Anthias macrophthalmus*, photo); ZMB 10599,1: 54.4 mm SL (holotype of *Priacanthus schlegelii*). LINE ISLANDS: BPBM 25302,2. LACM 4277,2. MARQUESAS ISLANDS: BPBM 11780,1. MARSHALL ISLANDS: BPBM 25876,1; FMNH 44443,1; USNM 141759,4; USNM 142271,1. MAURITIUS: BPBM 20269,1; MCZ 5973,1; MCZ 6177,1; MCZ 6178,3. MOZAMBIQUE: RUSI 11418,1. NORTHERN TERRITORY AUSTRALIA: AMS 1.21947-001,1. NEW CALEDONIA: MNHN 1964-315,1; USNM 282937,1; VMM 1124,1: 275 mm SL (holotype of *Priacanthus longipinnis*). NICOBAR ISLANDS: SU 41727,1. PERSIAN GULF: USNM 265647,1. PHILIPPINES: CAS 52443,1; SU 13538,1; SU 13619,1; SU 13845,1; SU 20693,1; SU 27098,1; SU 27099,1; SU 27100,1; SU 29640,1; USNM 154086,1; USNM 154087,1; USNM 154088,1; USNM 183232,4; USNM 183235,2; USNM 183239,1; USNM 183240,1; USNM 184857,1; USNM 184858,1; USNM 184859,1; USNM 195094,3; USNM 56107,1; ZMUC J.3,1. QUEENSLAND: AMS I.19108-012,1; AMS I.19914-001,1; AMS IB.7457,1. RED SEA: BPBM 19771,2; CAS 55584,1; CAS 55585,1; RUSI 4147,1; USNM 166907,1; USNM 270275,1; USNM 270275,1 C&S; USNM 282896,1; USNM 282934,1; USNM 282941,1 C&S; ZMUC FORSSKAL 24,1: 183 mm SL (lectotype of *Sciaena hamrur*, photo). REUNION ISLAND: MNHN 1078,2; MNHN 1975-702,2; MNHN A.230,1; MNHN A.240,3. SAMOA: BPBM 27765,1. SEYCHELLES: ANSP 108326,2; ANSP 108329,2; MNHN 54-61,3; MNHN 737,4: 47–53 mm SL (syntypes of *Priacanthus fax*); MNHN 92-237,1; MNHN A.164,1; MNHN A.165,1: 210 mm SL (holotype of *Priacanthus speculum*). SOCIETY ISLANDS: ANSP 82388,2; USNM 282872,1. SOLOMON ISLANDS: USNM 109414,1. SOMALIA: USNM 285475,1; USNM 290663,15. SOUTH AFRICA: ANSP 89207,1; ANSP 90051,1; RUSI 10381,1; RUSI 11120,1; RUSI 11776,3; RUSI 11777,4; RUSI 11940,4; RUSI 2687,1; RUSI 9117,2; RUSI 9835,1; SU 31405,1; USNM 153509,1; USNM 289285,4; USNM 289286,1; USNM 289289,2; USNM 289290,1. SOUTH CHINA SEA: CAS 55037,1; USNM 282879,1. SUMATRA: ZMA 116.605,1;



ZMA 116.606,1. TAIWAN: USNM 183234,6; USNM 191178,8. THAILAND: CAS GVF 57-65,1; CAS GVF 60-204,1; ZMUC P4499,1. WESTERN AUSTRALIA: NTM S.10959-085,1; WAM P.14573,1; WAM P.14728,1; WAM P.14830-001,2; WAM P.24876,1; WAM P.26209-001,2; WAM P.26224-008,2; WAM P.26579-002,2; WAM P.5492,2; WAM P.5829-001,3; WAM 29374-001,2. LOCALITY UNKNOWN: ZMUC 21,1.

*Priacanthus macracanthus* Cuvier

Plate IIIi; Figures 3g, 12f

*Priacanthus macracanthus* Cuvier, 1829: 108 (Amboine, Indonesia).

*Priacanthus benmebari* Temminck and Schlegel, 1842: 19 (Japan).

*Priacanthus junonis* DeVis, 1885: 392 (Queensland).

**Diagnosis.**—A medium-sized (to perhaps 290 mm SL) member of *Priacanthus* distinguished from members of the *Priacanthus hamrur-blochii* species group by having a relatively well developed preopercular spine (reaching beyond posterior tip of interopercle) at all sizes and lacking a prominent, black basal spot on dorsal surface of pelvic fins (a dark, rusty brown area sometimes present basally). Distinguished from *P. fitchi* by presence of numerous rusty brown to yellowish spots in membranes of dorsal, anal and caudal fins, lack of creamy white in soft portions of dorsal and anal fins, and deeper, less tapered body. Distinguished from *P. tayenus* in lacking inky black spots in membranes of pelvic fins, presence of rusty spots in dorsal, anal and caudal fins, rounded (vs. more pointed) soft portions of dorsal and anal fins, and higher scale counts (LS = 79–87 vs. 56–73).

**Description.**—Based on 45 specimens, dorsal-fin rays X,13 (12–14); anal-fin rays III,14 (13–14); pectoral-fin rays 18 (18–19); scales in lateral series 79–87 (83.6); lateral-line scales 72–82 (77.6); vertical scale rows 45–52 (48.8), 8–12 above lateral-line, 37–44 below. Total gill rakers on first arch 23–29 (25.0), 19–25 on lower limb, 4–7 on upper.

General profile evident in Plate IIIi. Largest specimen examined 273 mm SL; Senta (1977) reports to 285 mm SL. Body tapering very slightly to beneath middle of soft portion of dorsal fin, and then abruptly to peduncle. Caudal fin truncate. Soft portions of dorsal and anal fins broadly rounded, of moderate length, subequal to eye diameter. Pectoral fins relatively short to moderately long, considerably shorter than or subequal to pelvic spine length. Pelvic fins usually reaching to or beyond first anal spine. Preopercular spine long in juveniles reaching to pelvic girdle, remaining well developed in adults, usually reaching to beyond tip of interopercle. Lacrymal and second infraorbital with fine serrations as in *P. sagittarius* (Fig. 5a). Scales of midlateral area with elevated posterior field expansive, equal in area to anterior field, with numerous small spinules (about 80–100+) on surface and along margin (Fig. 3g). Extrinsic swimbladder muscles essentially as in *P. hamrur* (Fig. 10b).

Body proportions are based on 30 specimens 130.7–232.7 mm SL. BD 327–370 (349), BW 116–169 (140), CPL 124–164 (146), CPD 067–080 (074), HL 289–339 (304), HD 284–325 (301), HW 153–185 (168), ORB 134–168 (143), IO 063–079 (069), SN 064–102 (080), JW 175–205 (184), D1L 112–171 (138), D2L 117–166 (148), AL 124–156 (140), PIL 167–228 (193), P2L 256–298 (280). Ontogenetic variation appears to be slight in this species, being notable only in interorbital distance which exhibits moderate negative allometry.

Color in life (based on transparencies and published plates) silvery red or pink on head and body; iris of eye red. About 15 dark spots sometimes evident along lateral line. Fins (except pectorals) pink. Dorsal- and anal-fin membranes each with 3–5 rusty-red to yellowish spots (dusky or faded completely in preservative);

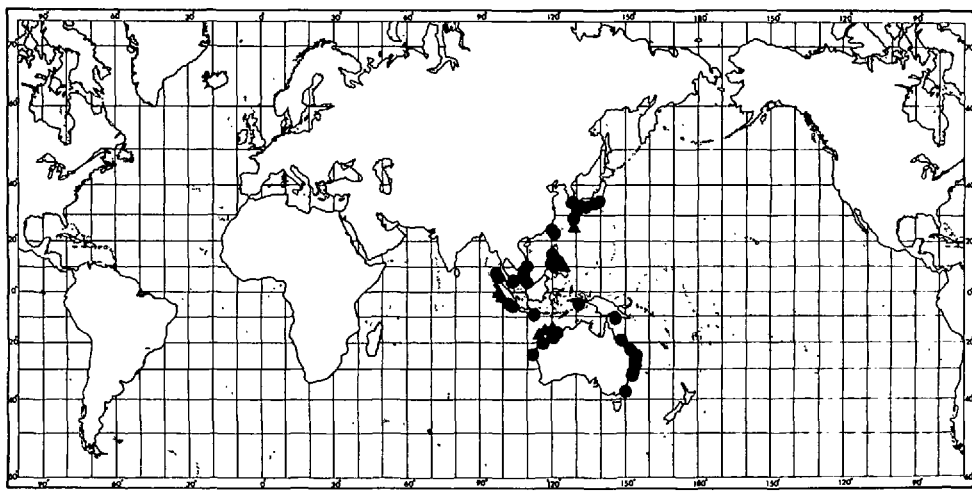


Figure 21. Distributions of *Priacanthus macracanthus* (circles) and *P. fitchi* (triangles).

pelvic fin membranes with small rusty spots, largest in membrane connecting fins to belly, and faint on distal one-fourth of fin; outer three pelvic membranes reddish, sometimes with a dark rusty blotch basally on dorsal surface, distal one-third sometimes dusky. Caudal fin dusky near margin and sometimes with rusty to light dusky blotches which form faint, irregular vertical rows. Mouth lined with reddish orange, gill rakers orange with white tips (T. Gloerfelt-Tarp, in litt.).

Pelagic juveniles (16–35 mm SL) (Fig. 12f) apparently dusky silvery on head and body. In 20 mm SL specimens, spinous dorsal-fin membranes, basal portions of anterior 2–3 soft dorsal membranes, and distal four-fifths of pelvic fins dusky to black; spinous portion of dorsal fin with basal, medial and submarginal rows of darker spots in 16 mm specimen; remaining fins white or clear. In 35 mm SL specimen, black pigment confined to anterior three to four interspinal membranes of dorsal fin; pelvic fins dark dusky overall.

**Distribution.** — In western Pacific and eastern Indian oceans from Japan and Korea south to western and southeastern Australia, not represented by substantiated records west of the Andaman Sea (Fig. 21); apparently restricted to portions of Indian-Australian and Eurasian tectonic plates. Eggleston's (1974) depiction of range including Indian waters is possibly in error. Coleman's (1980) stated occurrence in the temperate waters of South Australia thus far not substantiated by specimens. Fowler (1928) and Fowler (1931) incorrectly synonymized *P. meeki* Jenkins, *P. helvolus* Jordan, Evermann and Tanaka and "*P. caroli*" Curtiss (see *P. hamrur* "Remarks") with *macracanthus*, thus creating erroneous records from Hawaii and Tahiti in central Pacific. Weber and de Beaufort (1929) incorrectly synonymized *P. fax* Cuvier with *P. macracanthus* resulting in a spurious Seychelles record.

**Geographic Variation.** — Variation is evident in meristics, morphometric data, and pigmentation over the geographic range of *P. macracanthus*. Specimens from the coastal region of eastern Australia exhibit higher gill-raker counts than those of other regions, averaging 28.2 versus about 25.0. Scale and fin-ray counts show no patterns of regional variation. Specimens from Indonesia have notably longer pectoral fins on the average than those of other regions ( $\bar{x}$  = 206 vs. 187), though

there is considerable overlap, and lesser but significant differences in head and caudal peduncle lengths which are longer and shorter respectively. Specimens from Indonesia and off the Great Barrier Reef of Australia usually have smaller and more numerous spots in the dorsal- and anal-fin membranes, having about five spots per membrane versus three or so in specimens from other regions, both to the north and to the south.

*Biological Notes.*—Occurs over a great range of depths from less than 20 m to 400 m or more. Like *tayenus*, this species apparently forms aggregations in open bottom areas and is very abundant and important in the trawl fisheries of the South China and Andaman seas (Senta, 1977; Wongratana, 1982); it is of lesser incidence in the trawl fisheries of southern Australia (Coleman, 1980). Renzhai and Suifen (1982) studied the early development of *macracanthus* from the South China Sea and reported postlarvae captured from March to December; eggs are spherical and buoyant. Senta (1977) reports a recruitment and growth pattern similar to that of *P. tayenus*. Tremendous aggregations of juveniles, which had fed on planktonic crustacea, were reported from Philippine waters in March (Senta, 1978), indicating midwater feeding habitat. In winter, juveniles are common in shallow water in Australia (Marshall, 1965). Sound production has been studied in this species by Moulton (1962) and Walls (1964).<sup>1</sup>

*Remarks.*—The apparent mosaic pattern of regional distinctions between populations of *P. macracanthus* discussed above under "Geographic Variation," the unusually broad range of gill raker counts, and the seemingly great range of depths inhabited by this species relative to other species of *Priacanthus*, raise questions regarding possible polytypy, or even polymorphism. However, discordance between patterns of variation on a regional basis (i.e., pigmentation compared to meristics and morphometry) and overlap of key characters confounds the overall significance of these differences. The generally poor condition of trawl specimens from key areas greatly hinders a more rigorous comparison of morphometric and pigmentation characters and further study of this problem must await the availability of critical material.

See "Remarks" under *P. fuchi* regarding problems in distinguishing these species.

The type specimens of *Priacanthus benmebari* Temminck and Schlegel (1842) and *P. junonis* DeVis (1885) are apparently no longer extant but the description and plate of *benmebari* and description of *junonis* are clearly referable to *P. macracanthus*.

*Material Examined.*—144 specimens, 16–273 mm SL. AUSTRALIA: AMNH A.4051,1. CHINA: ANSP 91029,1; CAS GVF 1760,3; CAS GVF 1807,1; USNM 130618,1; USNM 85995,1; USNM 86034,2. EAST CHINA SEA: CAS 17564,1. INDONESIA: ANSP 151687,1; BMNH 1987.5.30:1–2,2; BMNH 1987.6.1:6,1; BMNH 1987.6.1:7,1; BMNH 1987.6.1:8,1; BMNH 1987.6.1:9–12,4; BMNH 1987.6.1:13–15,3; BMNH 1987.6.1:16–18,3; MNHN A. 174,1:150 mm SL (holotype); USNM 263759,1. JAPAN: AMNH 882,1; AMNH 883,1; CAS 22836,2; CAS 50014,1; CAS 50015,1; CAS 50016,1; CAS 50017,1; CAS 61721,1; FMNH 76864,1; FRLM 4588,1; RMNH 323,3; RMNH 5551,7; SU 22778,1; USNM 75474,1; USNM 76000,1; USNM 285021,1; USNM 285022,1; USNM 285023,1; USNM 285024,1. KOREA: FMNH 55753,1; MCZ 47713,1; SU 26529,1. NEW SOUTH WALES: AMS I.17203-002,7; AMS I.17875-006,4; AMS I.17887-004,1; AMS I.19199-004,1; AMS I.21819-001,1; AMS I.B.4184,1; LACM 42623-5,2; ROM 38684,1; SU 9187,1; USNM 42022,1; USNM 177108,1. NEW GUINEA: KFRS F.O. 1059,2; KFRS F.O. 1280,1; KFRS F.O. 186,2; KFRS F.O. 327,2; KFRS UNREG.,11. PHILIPPINES: CAS 32894,1; CAS 52465,1; USNM 122938,2; USNM 183154,1; USNM 183155,1; USNM 183206,1; USNM 282875,1; USNM 282939,3 (1 C&S). QUEENSLAND: AMS I.11041-3,3; AMS I.A.619,1; ANSP 95528,2; QM I.18535,2; QM I.18576,1;

<sup>1</sup> Walls, P. D. 1964. The anatomy of the sound producing apparatus of some Australian fishes. Unpub. Thesis, Bowdoin College.

QM I.18630,2; QM I.18694,1; QM I.18766,1; QM I.18787,1; QM I.18792,1; QM I.18818,1; QM I.18892,1; QM I.18960,1; QM I.18975,1; QM I.18988,1; QM I.19287,1; QM I.21323,1; QM I.9149,1; WAM P.25738-008,2; WAM P.29324-001,2. SOUTH CHINA SEA: CAS GVF 1774,1. TAIWAN: CAS 15872,6; CAS 28186,5; CAS 30015,1; CAS 34220,1; USNM 192571,2; USNM 85483,1. VICTORIA: AMS IB.7940,1. WESTERN AUSTRALIA: WAM P.2675-002,2; WAM P.26208-026,1. LOCALITY UNKNOWN: ZMUC 23,1.

*Priacanthus meeki* Jenkins

Plate II*d*; Figure 2*f*

*Priacanthus meeki* Jenkins, 1904: 450 (Honolulu, Hawaii).

*Priacanthus helvolus* Jordan, Evermann and Tanaka, 1927: 664 (Honolulu, Hawaii).

**Diagnosis.**—A relatively large (to perhaps 275 mm SL) member of *Priacanthus hamrur-blochii* species group diagnosed by an obsolescent preopercular spine in adults and black basal spot on pelvic fins. A member of the *hamrur* subgroup (along with *arenatus* and *prolixus*) defined by a crescentic caudal fin and increased median fin-ray counts (usually 14 vs. 13 and 15 vs. 14 soft dorsal and anal rays respectively). Distinguished from very similar subgroup member *P. hamrur* of the Indo-Pacific by higher scale (LS 104–115 vs. 79–96, VSR 61–67 vs. 48–58), gill raker ( $\bar{x}$  = 31.4 vs. 25.1), and pectoral ray ( $\bar{x}$  = 19.2 vs. 18.3) counts. Distinguished from *P. arenatus* of Atlantic and *P. prolixus* of Indian Ocean by higher scale counts (LS 83–93 in those species) and, further from *prolixus*, by greater body depth ( $\bar{x}$  = 370 vs. 326).

**Description.**—Based on 20 specimens, dorsal-fin rays X, 14 (14–15); anal fins III, 15 (14–16); pectoral-fin rays 19 (19–20). Scales in lateral series 104–115 (108.8); lateral-line scales 80–93 (87.3); vertical scale rows 61–67 (63.8), 13–16 above lateral-line, 47–51 below. Total gill rakers on first arch 30–33 (31.4), 23–25 on lower limb, 7–8 on upper. See "Remarks" below regarding counts of possible *meeki* specimen from Galapagos Islands.

General profile evident in Plate II*d*. Largest specimen examined 255 mm SL. Caudal fin crescentic. Soft portions of dorsal and anal fins broadly rounded, moderately long, slightly exceeding eye diameter. Pectoral fins relatively short and broadly pointed, shorter than pelvic spines. Pelvic fins usually reaching to anal spines 2–3. Preopercular spine obsolescent in adults. Lacrymal and second infraorbital with fine serrations as in *P. sagittarius* (Fig. 5*a*). Scales of midlateral region with elevated posterior field about one-half area of anterior field, more or less parallel sided, with about 50–70 spinules on margin and surface (Fig. 2*f*). Extrinsic swimbladder muscles situated as in *P. hamrur* (Fig. 10*b*).

Body proportions based on 20 specimens 86.8–255.0 mm SL. BD 329–434 (370), BW 125–166 (144), CPL 119–149 (133), CPD 068–089 (081), HL 274–327 (306), HD 288–369 (324), HW 135–183 (166), OR 121–161 (140), IO 069–084 (077), SN 080–096 (087), JW 165–206 (189), D1L 125–171 (148), D2L 129–172 (156), AL 129–192 (158), P1L 133–188 (170), P2L 175–313 (259). Ontogenetic variation is evident in several distance measurements. Relative body depth on the average increases with age and there are slight increases in body width, caudal peduncle depth, and lengths of soft portions of dorsal and anal fins. Head and lower jaw length and orbit diameter are negatively allometric.

Color in life (based on transparencies of live specimens) red on head, iris of eye, body and fins, about 15 darker red spots sometimes evident along lateral-line. Dorsal, anal and caudal fins dusted with melanophores, darkest near borders. Pectoral fins clear or slightly pink; pelvic-fin membranes dusky, especially distally, with black spot basally on dorsal surface. Evidence of silver-red blotched color

phase or fin spotting described for very similar *P. hamrur* has not been observed in this species.

Pelagic juvenile specimens are not available but are probably pigmented similarly to the closely related *P. hamrur* and *P. arenatus*.

*Distribution*.—Hawaiian Islands, including Midway (Fig. 20). A single juvenile specimen from the Galapagos Islands in the eastern Pacific may represent this species (but see Remarks below). Jordan and Hubbs (1925) incorrectly record this species from Japan, probably based on *hamrur*.

*Biological Notes*.—Recorded from relatively shallow depths of as few as 3 m to perhaps 50 m. Seems to occupy a generally shallower depth range than the syntopic *P. alalaua*. Based on dissection of gonads, spawning may occur by December or soon after. Sound production in this species has been studied by Salmon and Winn (1966).

*Remarks*.—A single juvenile specimen (USNM 135644, 41.7 mm SL) (not included in descriptive data above) from the Galapagos Islands of the eastern Pacific is here treated with *meeki*. The specimen clearly represents the *hamrur* subgroup and has gill raker (31) and pectoral-fin ray (20) counts within the range of *meeki*; however, overall meristics, including scale counts (LS 93, VSR 57), are suggestive of *arenatus* of the Atlantic (thus may key to *arenatus* herein). Pending a better estimate of variation in the eastern Pacific population, this specimen is tentatively referred to *meeki* with the contention that the Galapagos population may have lower (but possibly overlapping) scale counts than Hawaiian populations. As such, the distribution of *meeki* may correspond in part to that of *P. alalaua*, another species thought endemic to the Hawaiian region until recently. Considering the shallow depth preferences of all members of the *hamrur* subgroup, and the relative ease of collecting, it is troublesome that specimens have not been recorded from elsewhere in the relatively well collected eastern Pacific. The single specimen may represent a distinct taxon questionably restricted to the northern Nasca Plate region in the Galapagos. Additional material is needed to resolve its status.

In Hawaii, *P. meeki* has been oddly confounded with *P. macracanthus* by several authors (Fowler, 1928; 1931; Tinker, 1944), a species which it little resembles. This has resulted in spurious Hawaiian records for the latter species.

The holotype of *P. meeki* (USNM 50847) is apparently lost as is the type of *Priacanthus helvolus* Jordan, Evermann and Tanaka (1927) (CAS 390). The identities of both nominal taxa are clear based on good illustrations and data in the original descriptions and both agree with two remaining paratypes of *meeki* (USNM 126123).

*Material Examined*.—98 specimens, 48–255 mm SL. GALAPAGOS ISLANDS: USNM 135644,1 (questionably *meeki* or undescribed form). HAWAIIAN ISLANDS: eastern islands, AMNH 7479,1; ANSP 31795,1; ANSP 51379-80,2; ANSP 51390,1; ANSP 89261,1; BPBM 1828,2; BPBM 1829,1; BPBM 20879,1; BPBM 24181,3; BPBM 3995,1; BPBM 6456,1; BPBM 31880,1; CAS 12800,1; CAS 17715,1; CAS 390,1; FMNH 4263,1; FMNH 59336,1; LACM 310,1; MCZ 16744,5; MCZ 31468,2; SU 6039,2; SU 8121,3 (1 C&S); USNM 126123,2 (paratypes); USNM 160670,2; USNM 161693,2; USNM 164624,1; USNM 17994,32; USNM 183236,1; USNM 282883,1; USNM 50847,1; USNM 51077,1; USNM 52810,1; USNM 82851,1; USNM 82864,2; USNM 82866,1; USNM 92255,1. Midway Island, CAS 52078,13.

### *Priacanthus nasca* new species Starnes Plate IIIa

*Holotype*.—BPBM 30544, 268 mm SL female, Easter Island, off Hanga Roa, hook and line, A. C. Agana (procured by J. E. Randall), 10 February 1985.

*Paratypes*.—BPBM 30924, 182 mm SL, Easter Island, Motu Tautara, 40 m, spear, J. E. Randall, 16 February 1986; CAS 60363, 180 mm SL, same data as BPBM 30924 except 7 February 1986; MNHN 1987-934, 176 mm SL, same as BPBM 30924 except 12 February 1986; USNM 284066, 199 mm SL, same as previous; USNM 284067, 237 mm SL, same data as holotype.

*Diagnosis*.—A relatively large (to perhaps 275 mm SL) member of *Priacanthus hamrur-blochii* species group defined by an obsolescent preopercular spine in adults and black basal spot on pelvic fins. A member of the *blochii* subgroup (also including *alalaua* and *sagittarius*) characterized by thicker, less tapered gill rakers (Fig. 18a) and reduced gill raker counts (23 or fewer). Distinguished from *alalaua* by higher scales counts (LS 89–94 vs. 72–84). Distinguished from *blochii* by longer pectoral fins (1.3–1.6 in head length vs. 1.9–2.2) and higher scale counts (LS 89–94 vs. 74–85). Distinguished from *sagittarius* by lacking black blotches in first two interspinous membranes of dorsal fin, having rounded versus broadly pointed soft portions of dorsal and anal fins, and higher scales counts (LS 64–74 in *sagittarius*).

*Description*.—Based on holotype and five paratypes, dorsal-fin rays X,13; anal-fin rays III,14; pectoral-fin rays 18–19. Scales in lateral series 89–94 (91.8); lateral-line scales 76–85 (81.1); vertical scale rows 59–63 (60.6), 11–13 above lateral-line, 46–50 below. Total gill rakers on first arch 21–23 (21.8), 16–17 on lower limb, 4–6 on upper.

General profile evident in Plate IIIa. Largest specimen 268 mm SL. Caudal fin slightly emarginate. Soft portions of dorsal and anal fins broadly rounded, of moderate length, subequal to eye diameter. Pectoral fin relatively long and broadly pointed, equal to or exceeding pelvic spine length. Pelvic fin reaching to or beyond anal-fin origin except in largest specimen. Preopercular spine reduced, not quite reaching tip of interopercle. Lacrymal and second infraorbital with fine serrations as in *P. sagittarius* (Fig. 5a). Extrinsic swimbladder muscles situated as in *P. hamrur* (Fig. 10b). Midlateral scales essentially identical to *P. alalaua* (Fig. 3a, b).

Body proportions for six types are: BD 367–408 (378), BW 143–175 (162), CPL 132–159 (143), CPD 079–083 (081), HL 302–346 (323), HD 322–365 (333), HW 172–213 (190), OR 121–170 (150), IO 075–091 (083), SN 080–095 (089), JW 171–200 (190), D1L 133–162 (150), D2L 153–177 (162), AL 138–167 (152), P1L 196–217 (206), P2L 269–320 (297). On the basis of six specimens, it appears that there may be ontogenetic variation in some morphometric distances. There is apparent positive allometry, particularly in larger specimens, in proportional head and body width. Negative allometry occurs in lengths of several fins, most notably the spinous portion of dorsal fin and pelvic fins and, to a lesser degree, soft portions of dorsal and anal fins.

Color in life (based on transparencies of live and fresh-caught specimens) red blotched with silvery on head, iris of eye, body and fins. About 15 small dark spots are evident along lateral line. Dorsal, anal and caudal fins lightly dusted with melanophores, darker near fringes; pectoral fin clear or slightly pink. Pelvic fin membranes dark on distal two-thirds with black spot basally on dorsal surface. A blotched color phase has not been observed in this species.

*Distribution*.—Known only from the types from Easter Island in the eastern Pacific (Fig. 19). Probably endemic to islands and seamounts of the southwestern Nasca Plate region.

*Biological Notes*.—All specimens for which depth information is available have been taken at depths of 30–40 m along rocky drop-offs. Larger specimens were

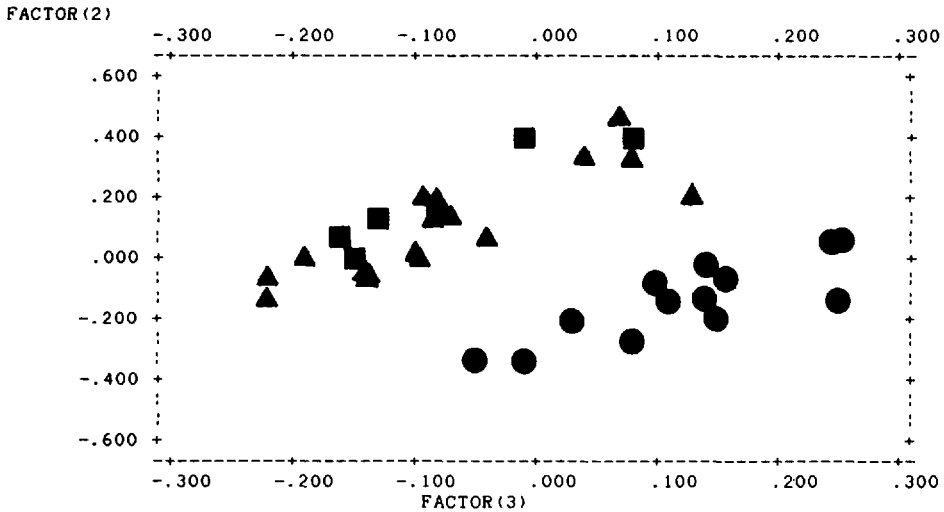


Figure 22. Graphed results of principal components analysis of morphometric distances in *Priacanthus blochii* (circles), *P. alalaua* (triangles), and *P. nasca* (squares).

taken on hook and line at undetermined but deeper depths over bottoms of about 240 m. All six specimens (1 male, 5 females) have been collected during February and appear to be nearing spawning condition based on condition of the gonads.

**Remarks.**—*Priacanthus nasca*, *P. blochii* and *P. alalaua* are a phenetically similar triad of species. While *P. nasca* and *P. alalaua* are hypothesized to be sister species based on two shared, presumably derived, conditions (see “Phylogenetic Analysis”), *P. nasca* and *P. blochii* of the Indo-West Pacific region are actually more difficult to distinguish from one another. The apparent east-west cline in scale counts discussed under *P. blochii* raised questions as to whether the higher counts of the Easter Island population might represent the eastern terminus of this cline which increases from west to east. However, the lack of similar trends in distinctive morphometric characters and the apparent allopatry of these forms indicate that two taxa are involved. Principal components analysis performed on morphometric distances for the three species (Fig. 22) revealed significant differences in shape between *P. nasca* and *P. blochii* with the hypothesized sister species *nasca* and *alalaua* in fact grouping together. Heaviest factor loadings along PC II and PC III resulting in this separation are for head width, orbit diameter, anal- and pectoral-fin lengths, the latter being one of the hypothesized synapomorphies uniting *nasca* and *alalaua*. In addition to elongate pectoral fins and reduced upper jaw lengths, *P. nasca* and *P. alalaua* also share a more truncate to slightly emarginate caudal fin compared to the rounded fin of *P. blochii*.

**Etymology.**—*nasca* is a noun in apposition referring to the Nasca lithospheric plate region to which this form is probably endemic. The name is originally derived from a pre-Columbian culture of coastal Peru.

### *Priacanthus prolixus* new species Starnes

Figure 23a, b

**Holotype.**—USNM 290660, 210.2 mm SL, female, Indian Ocean, off Somalia (Baargaal), 11°21'06"N, 51°09'06"E, trawled 37 m, G. J. Small, 1 May 1987.



Figure 23. *Priacanthus prolixus* new species. a) holotype, USNM 290660, 210.2 mm SL, Somalia; b) paratype, USNM 284068, 149.6 mm SL, Pakistan.

*Paratypes*. — ANSP 53131, 163.0 mm SL, India, Bombay fish market, F. Fallberg, 1924; BPBM 27730, 5:99.1–239.0 mm SL, India, Kerala State, Vizhinjam, J. E. Randall (from fishermen), 15 February 1980; USNM 284068, 149.6 mm SL, Pakistan, Karachi fish market, G. Bianchi, 1984; USNM 285474, 121.0 mm SL, Indian Ocean, Somalia, Ras Binnah, 11°04'48"N, 51°11'12"E, trawl 65 m, G. J. Small, 17 October 1986; USNM 290661, 153.2 mm SL, off Somalia, 11°9'48"N, 47°43'24"E, trawl, G. J. Small, 10 February 1986; USNM 290662, 210.0 mm SL, off Somalia, 10°39'18"N, 51°18'48"E, trawl, G. J. Small, 16 October 1985. USNM 291682, 187.0 mm SL, Gulf of Aden, 10°51'40"N, 43°56'35"E, trawl 258–326 m, J. June and G. J. Small, 6 September 1986.

*Non-type Material*. — USNM 6534, 218.0 mm SL, China, Hong Kong, W. Stimpson, date unknown.

*Diagnosis*. — A medium-sized (so far as known) (to perhaps 250 mm SL) member of the *Priacanthus hamrur-blochii* species group diagnosed by an obsolescent preopercular spine in adults and black basal spot on pelvic fins. A member of the *hamrur* subgroup (also including *arenatus* and *meeki*) defined by a crescentic caudal fin and increased median fin ray counts (modally 14 vs. 13 and 15 vs. 14 soft dorsal- and anal-fin rays respectively). Distinguished from *P. meeki* of the Hawaiian Islands by lower scales counts (LS 86–93 vs. 104–115) and more elongate body. Distinguished from *P. arenatus* of the Atlantic by more elongate (less deep) body ( $\bar{x}$  = BD 326 vs. 362) and fewer vertical scale rows ( $\bar{x}$  = 47.5 vs. 53.4). Distinguished from the sympatric *P. hamrur* by higher gill raker counts (total on first arch 29–31 vs. 24–26), fewer vertical scale rows ( $\bar{x}$  = 47.5 vs. 53.6), and much more elongate body ( $\bar{x}$  = BD 326 vs. 379).

*Description*. — Based on holotype and 10 paratypes, dorsal-fin rays X, 14 (13–14); anal-fin rays III, 15 (14–15); pectoral-fin rays 19 (18–21). Scales in lateral series 86–93 (89.1); lateral-line scales 75–82 (79.3); vertical scale rows 44–51 (47.5), 8–



11 above lateral line, 35–40 below. Total gill rakers on first arch 28–31 (29.0), 22–24 on lower limb, 6–7 on upper.

General profile evident in Figure 23. Largest specimen examined 239 mm SL. Caudal fin crescentic. Soft portions of dorsal and anal fins broadly rounded, of moderate length, not exceeding eye diameter on specimens examined thus far. Pectoral fins relatively short and broadly pointed, shorter than pelvic spines. Pelvic fins usually reaching to or slightly beyond anal-fin origin. Lacrymal and second infraorbital with fine serrations as in *P. sagittarius* (Fig. 5a). Midlateral scales as described for *P. meeki* (Fig. 2f). Extrinsic swimbladder muscles situated as in *P. hamrur* (Fig. 10b).

Body proportions are based on 10 specimens 99–239 mm SL. BD 289–343 (326), BW 130–162 (141), CPL 121–157 (140), HL 294–305 (287), HD 264–305 (287), HW 143–175 (158), ORB 113–141 (128), IO 066–079 (070), SN 071–091 (083), JW 151–194 (177), D1L 115–182 (142), D2L 121–197 (153), AL 119–165 (146), P1L 163–195 (181), P2L 248–302 (277). Ontogenetic variation is apparent in lengths of soft portions of dorsal and anal fins and pelvic fins which average slightly more in adults.

Color in life has not been observed by the author but is presumably predominantly reddish as in all other species of *Priacanthus* and probably approximates that described for closely related species such as *P. hamrur* and *P. arenatus*. Dorsal, anal and caudal fins are dark to light dusky on distal one-fifth. Soft portions of dorsal and anal fins in two specimens show evidence of small dark spots in membranes. Pelvic-fin membranes dusky, nearly black on distal one-third. Juvenile pigmentation is not known but probably approximates that described for *P. arenatus*.

*Distribution.*—Definitely recorded from, and possibly restricted to, northwest Indian Ocean (Arabian Sea, Gulf of Aden). Records are from off Somalia, India and Pakistan (Fig. 20). However a probable specimen of *prolixus* (USNM 6534) is ostensibly from Hong Kong, China. Extent of distribution in the Indo-Pacific is thus imperfectly known. Confusion of *P. prolixus* with the similar *P. hamrur* will probably impede a better understanding of its distribution for years to come.

*Biological Notes.*—Most specimens for which capture information is available were trawled from depths of 35 and 65 m over presumably relatively open bottom; one is from over 250 m. These were taken with or in the vicinity of specimens of *P. hamrur*. Larger specimens of both *prolixus* and *hamrur*, captured during May, appeared to be near spawning based on condition of the gonads and may represent a spawning aggregation. If the habits of *prolixus* are similar to those of its hypothesized close relatives (*hamrur* subgroup), it may occur more commonly near reefs and rock formations much of the time.

*Remarks.*—The first specimen of *Priacanthus prolixus*, from Pakistan, was brought to my attention by G. Bianchi (FAO). It is here interpreted as a cryptic, and possibly relatively uncommon, species which has been confused with the similar and presumably closely related sympatric species, *P. hamrur*. An alternate hypothesis is that *P. hamrur* is exhibiting polymorphism in gill raker morphology coincident with altered body shape resulting in the form here described as *prolixus*. Neither hypothesis can be tested without detailed ontogenetic information on many specimens of known parentage, data that will be extraordinarily difficult to obtain for priacanthids. The much higher, non-overlapping, gill raker counts of *P. prolixus* relative to *P. hamrur* are believed to be a co-derived condition shared with *P. arenatus* and *P. meeki*, which are thus hypothesized to be its nearest

relatives (see "Phylogenetic Analysis"). This argument, in addition to the consistent differences outlined in the "Diagnosis," supports a hypothesis of species status for this form.

In addition to differences between *P. prolixus* and *P. hamrur* in gill raker counts, vertical scale row counts and body depth outlined in the "Diagnosis," other differences reflecting the more attenuate body form of *prolixus* are lesser head depth ( $\bar{x}$  = 287 vs. 326) and caudal peduncle depth (076 vs. 086). Though variable and based on a small sample of adults, it appears that lengths of soft portions of the dorsal and anal fins average considerably less in *prolixus* ( $\bar{x}$  = 153 vs. 175 and 146 vs. 167 respectively). Pectoral-fin ray counts average higher in *prolixus* (19.2 vs. 18.3).

*Etymology.*—"prolixus," a Latin word meaning "stretched out" or "long," in reference to the relatively attenuated body of this species.

***Priacanthus sagittarius* new species Starnes**  
Plates IIIe–g; Figures 3f, h, 5a–d, f, 8b, 12c, 18b

*Holotype.*—USNM 285042, 225 mm SL, male, Indonesia, Sumatra, off south coast, 06°13'00"S, 104°38'45"E, 42 m, trawl, T. Gloerfelt-Tarp, 30 April 1983.

*Paratypes.*—AMNH 77349, 2:90–110 mm SL, Red Sea, Ethiopia, Massawa, 79 m, trawl, L. Knapp, 20 September 1971; AMS I.26840-001, 2:103–107 mm SL, same as AMNH 77349; ANSP 151675, 2:23–31 mm SL, Indonesia, 08°40'S, 114°40'E, midwater trawl to 440 m, R/V JURONG, Cr. 25, Sta. 473, 10 March 1981; ANSP 151676, 47 mm SL, Indonesia, 07°32'S, 106°32'E, midwater trawl, R/V JURONG, Cr. 19, 14–23 October 1980; ANSP 151677, 3:27–34 mm SL, Indonesia, 09°06'S, 114°40'E, trawled at surface, R/V JURONG, Cr. 25, Sta. 477, 11 March 1981; ANSP 159039, 3:96–109 mm SL, same as AMNH 77349; BMNH 1987.6.1:2–3, 2:189–199 mm SL, Indonesia, Bali-Java, off south coast, trawl, P. J. Whitehead, 1979; BMNH 1987.6.1:1, 261 mm SL, 8°50'S, 114°14'E, trawl, P. J. Whitehead, 14 July 1979; BPBM 19473, 253 mm SL, Indonesia, Molucca Islands, Ambon, fish market, J. E. Randall, 6 February 1975; BPBM 31882, 3:102–118 mm SL, same as AMNH 77349; CAS 54998, 69 mm SL, Philippines, Batangas, West Fortune Island, A. Herre, 2 October 1947; CAS 60360, 3:104–173, same as AMNH 77349; CSIRO CA 1286, 263 mm SL, Western Australia, east of Ashmore Reef, 88 m, trawl, G. Leyland, 31 March 1981; CSIRO CA 1498, 102 mm SL, Western Australia, northwest of Roebuck Bay, 52 m, trawl, G. Leyland, 8 November 1980; FMNH 97122, 180 mm SL, same as BMNH 1987.6.1:2; FRLM 2469, 132 mm SL, Japan, Mie Prefecture, Shima-cho, off Katada, set net, 6 March 1980; HUJ F.11152, 252 mm SL, Red Sea, Israel, Eilat, 250–300 m, A. Diamant, June 1982; LACM 44286-1, 2:97–109 mm SL, same as AMNH 77349; MNHN 4095, 276 mm SL, Isla Reunion, Malavois, 1866; MNHN 1987-933, 3:92–104 mm SL, same as AMNH 77349; NTM S.10996.005, 2:88–96 mm SL, Indonesia, Sumatra, off south coast, 03°24'30"S, 100°33'30"E, trawl, T. Gloerfelt-Tarp, 2 May 1983; NTM S.11021-001, same as BMNH 1987.6.1:2; QM I.22744, 3:78–86 mm SL, same as NTM S.10996.005; RMNH 30584, 2:106–115 mm SL, same as AMNH 77349; TMBS 851103-1, 138 mm SL, Japan, Miyake-jima, Ako, 28 m, trap net, fishermen (procured by J. Moyer), 3 November 1985; USNM 236936, 193 mm SL, Samoa, Tutuila Island, Pago Pago, 100 m, fisherman W. Pedro (procured by R. Wass), 3 September 1982; USNM 263757, 205 mm SL, Indonesia, Sumatra, off south coast, 04°07'00"S, 101°04'30"E, 45 m, trawl, T. Gloerfelt-Tarp, 5 February 1983; USNM 283769, 5:33–176 mm SL, same as AMNH 77349; USNM 283768, 155 mm SL, same as AMNH 77349 except 35–37 m, 19 September 1971; USNM 283767, 2:251–256 mm SL, Sri Lanka, 09°57'N, 80°37'E, trawl, M/V BERUWALLE, F. Schwartz, 11 March 1969; USNM 285045, 43 mm SL, Indonesia, Sumatra, off south coast, 06°07'S, 104°39'E, 34 m, trawl, T. Gloerfelt-Tarp, 30 April 1983; USNM 285043, 73 mm SL (C&S), Indonesia, Sumatra, off south coast, T. Gloerfelt-Tarp, 1983; WAM P.29373-001, 175 mm SL, same as BMNH 1987.6.1:2; ZMA 116.604, 143 mm SL, "Indische Archipelago," no further data.

*Diagnosis.*—A relatively large (to perhaps 290 mm SL) member of *Priacanthus hamrur-blochii* species group diagnosed by an obsolescent preopercular spine in adults and black basal spot on pelvic fins. A member of the *blochii* subgroup (including also *alalaua* and *nasca*) characterized by thicker, less tapered gill rakers (Fig. 18a) and reduced gill raker counts (23 or less). Distinguished from all mem-

bers of *hamrur-blochii* species group by presence of black blotches in first two interspinal dorsal-fin membranes, longer posterior dorsal spines (tenth about 2.0 length of second vs. 1.5–1.7), longer, more pointed soft dorsal and anal fins, and lower scale counts (LS 67–74 vs. 72–94 in other species).

*Description.* — Based on 20 specimens, dorsal-fin rays X, 13–14; anal-fin rays III, 14–15 (13–15); pectoral-fin rays 18 (17–19); scales in lateral series 67–74 (71); lateral-line scales 62–72 (66.1); vertical scale rows 46–53 (49.6), 8–12 above lateral-line, 37–42 below. Total gill rakers on first arch 19–22 (20.6), 15–17 on lower limb, 3–5 on upper.

General profile evident in Plate IIIe, f. Largest specimen examined 279 mm SL. Caudal fin rounded. Soft portions of dorsal and anal fins relatively long (about 1.5 times eye diameter) and broadly pointed. Pectoral fins relatively short and broadly pointed, shorter than pelvic spines. Pelvic fins usually reaching to or beyond third anal spine. Preopercular spine obsolescent in large adults, reduced to a triangular prominence or scarcely evident. Lacrymal and second infraorbital with fine serrations (Fig. 5a). Midlateral scales of young with well developed apical field bearing 20–25 spinules (Fig. 3f) ontogenetically receding to a spineless, pointed flange in adults (Fig. 3h). Extrinsic swimbladder muscles positioned as in *P. hamrur* (Fig. 10b).

Body proportions are based on 16 specimens 155–263 mm SL. BD 381–432 (399), BW 143–174 (160), CPL 124–167 (145), CPD 084–104 (094), HL 273–352 (324), HD 336–384 (358), HW 172–193 (185), OR 139–167 (154), IO 064–084 (073), SN 088–109 (096), JW 200–225 (208), D1L 146–191 (171), D2L 194–273 (241), AL 185–260 (229), P1L 176–212 (194), P2L 304–361 (342). Ontogenetic variation appears to be relatively minimal in this species, being notable only in soft dorsal- and anal-fin lengths which become on the average longer with maturity.

Color in life (based on transparencies of freshly killed or live specimens) reddish-silvery on head and body or, alternately, pale yellowish with gray mottling (Pl. IIIg). Iris of eye pink to bright red. Dorsal, anal and caudal fins pink with reddish-brown spots in membranes or yellowish with dusky spots, less distinct in caudal. First two interspinal dorsal-fin membranes with oblique black blotches distally. Pelvic fins dusky, darkest on distal two-thirds, or lighter, with reddish brown or dusky spots in membranes, or creamy white with a yellow wash in central membranes; pelvics with a black spot basally on dorsal surface. Gill rakers white (T. Gloerfelt-Tarp, in litt.).

Pelagic juveniles (28–30 mm SL) (Fig. 12c) apparently plain silvery on body and head. Interspinal dorsal-fin membranes dark dusky, anterior membranes darkest; anterior three to four membranes of soft portion of dorsal fin black basally, remainder of fin clear or whitish, with or without dark specks. Membranes between anal spines with basal and submarginal blotches, continuing onto first two or three soft ray membranes; remainder of anal fin and caudal fin clear or whitish. Pelvic fins dark dusky overall.

*Distribution.* — Occurring widely in Indian and western Pacific oceans from Red Sea and Reunion east to Japan, northern Australia and Samoa (Fig. 24). Recorded from Pacific Plate only at Samoa.

*Biological Notes.* — Recorded from depths of 60 to 100 m in both rocky and more open bottom areas. Taken occasionally in trawls. A large series of juveniles (about 90–120 mm SL) (USNM 283769 and others) was trawled in the Red Sea during the month of September, probably indicating occurrence of juvenile aggregations.

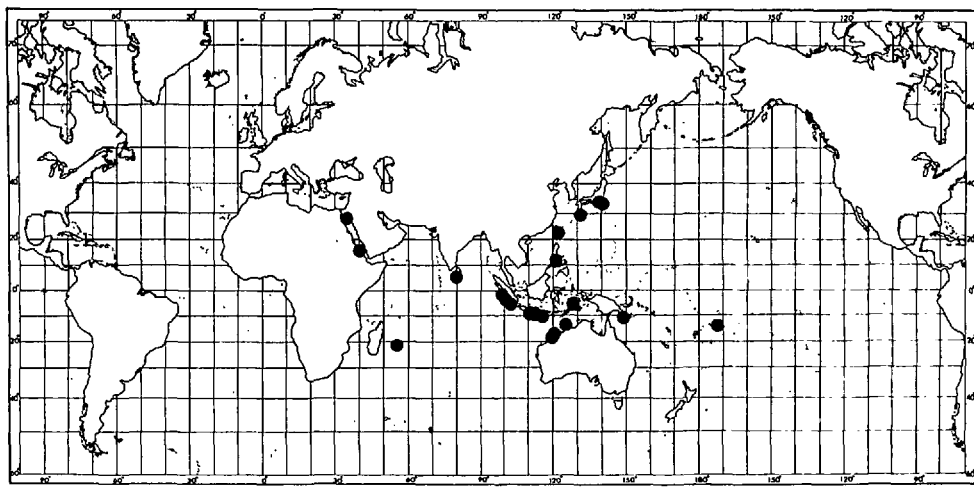


Figure 24. Distribution of *Priacanthus sagittarius*.

Smaller juveniles (23–34 mm SL, ANSP 151675, 151677) were taken in midwater trawls off Java in March; a specimen (ANSP 151676) collected from the same area in October had attained 47 mm SL. Gonads of large adults collected during December appear to be approaching spawning condition.

The somber color phase in this species (Pl. IIIg) may be a fright or stress response. It also possibly serves to camouflage under these conditions. The specimen illustrated had been held in a concrete aquarium for several hours at the marine laboratory in Eilat, Israel (A. Diamant, in litt.). Other priacanthids may be capable of such pigmentation changes under similar conditions.

*Remarks.* — The species epithet *blochii* Bleeker has been incorrectly applied to this form by several authors; see “Remarks” under *P. blochii* for clarification.

Masuda et al. (1975, 1984), Gloerfelt-Tarp and Kailola (1984), and Sainsbury et al. (1985) refer to this form as “Sp. 1”; it is “*P. sp.* (type 2)” of Kimura and Suzuki (1980).

*Etymology.* — *sagittarius* (Latin), meaning “of arrows,” in reference to the overall posterior configuration of this species, resulting from the pointed dorsal and anal fins and blunt caudal fin, which resemble the fletching and butt of an arrow.

*Priacanthus tayenus* Richardson  
Plate IIIj, k; Figures 3c, 5a, 10c, 12b

*Priacanthus tayenus* Richardson, 1846: 238 (Canton, China).

*Priacanthus holocentrum* Bleeker, 1849: 48 (Batavia, Indonesia).

*Priacanthus schmittii* Bleeker, 1852: 572 (Padang, Sumatra).

*Diagnosis.* — A relatively small (to perhaps 250 mm SL) member of *Priacanthus* distinguishable from its congeners by the presence of several inky black to brown spots in membranes of pelvic fins, lunate caudal fins (in some individuals), fewer and larger serrations on suborbital bones (Fig. 5a), configuration of extrinsic swimbladder muscle (Fig. 10c), and by having apical field of lateral body scales of adults reduced to a narrow spineless flange (Fig. 3c) rather than broad and bearing spines or reduced to a pointed flange.

*Description.*—Based on 30 specimens, dorsal-fin rays X, 12 (11–13); anal-fin rays III, 13 (12–14); pectoral-fin rays 18 (17–19); scales in lateral series 56–73 (65.2); lateral-line scales 51–67 (60.8); vertical scale rows 40–50 (45.5), 8–10 above lateral-line, 30–40 below; total gill rakers on first arch 21–24 (22.2), 17–19 on lower limb, 3–6 on upper.

General profile evident in Plate IIIj, k. Largest specimen examined 221 mm SL (Senta, 1977, reports to 245 mm SL). Caudal fin rounded (in young), truncate, or lunate with outer rays greatly produced (Pl. IIIk), possibly only in males. Soft portions of dorsal and anal fins angulate to pointed (rays 6–9 produced), length much exceeding eye diameter. Pectoral fins relatively short and broadly pointed, shorter than or subequal to pelvic spine length. Pelvic fins reaching to or beyond anal-fin origin. Preopercular spine very long in young, reaching beyond pelvic girdle, and remaining relatively well developed in adults, usually extending to or beyond tip of subopercle. Lacrymal and second infraorbital bones with large serrations (Fig. 5a). Midlateral body scales with elevated posterior field expansive and bearing about 20–25 spines in small juveniles (<50 mm SL) as in *P. sagittarius* (Fig. 3f); field receding ontogenetically and represented by narrow, spineless flange in adults (Fig. 3c). Extrinsic swimbladder muscles (Fig. 10c) relatively massive, inserted ventrally on swimbladder, and connected ventrally to contralateral muscle beneath bladder by broad ligamentous band which is mostly free of attachment except for a narrow median adherence.

Body proportions are based on 20 specimens 104–221 mm SL. BD 319–396 (354), BW 129–161 (142), CPL 138–175 (158), CPD 085–099 (092), HL 316–354 (330), HD 294–340 (317), HW 168–197 (180), ORB 147–175 (159), IO 053–073 (061), SN 077–098 (088), JW 191–233 (208), D1L 125–159 (140), D2L 169–297 (245), AL 161–220 (185), P1L 157–200 (179), P2L 252–344 (299). Ontogenetic variation is evident in several morphometric distances. Snout and jaw length show marked negative allometry; soft portion of dorsal fin often greatly produced in half grown specimens but more broadly angulate in larger specimens, length thus being negatively allometric over size range of specimens measured (small juveniles have this fin relatively short and angulate) (Fig. 12b).

Color in life (based on transparencies and published plates) silvery pink on head and body; iris of eye red; all fins except pectorals creamy pink or orangish; pectoral fins clear to slightly yellowish. Dorsal, anal and caudal fins lacking spots or blotching. Membranes of spinous portion of dorsal fin and anterior three to four membranes of soft portion lightly dusted with melanophores; soft portion of anal fin dusted with melanophores on distal one-fifth of first five to six interradial membranes. Pectoral fins clear to slightly yellowish; pelvic fins with milky cast, often persisting in preservation; inner three pelvic-fin membranes and connective membrane between fins and belly with numerous inky black or brown blotches which are largest and fewer in number in more medial membranes; outer two membranes dusky.

Pelagic juveniles (Fig. 12b) dusky silvery on head and body. Interspinal membranes of dorsal fin dark dusky, sometimes with darker blotches medially and near base. Soft portions of dorsal and anal fins clear or whitish except anterior 2–3 interradial membranes of dorsal fin dusky in some specimens. Caudal fin clear or whitish, sometimes with about four faint dusky vertical bands. Pelvic fin membranes dusky, variously blotched; membranes between pelvic fins and belly with two or three black blotches.

*Distribution.*—Northern Indian and western Pacific oceans (Fig. 25); confined generally to Indian-Australian and Eurasian tectonic plate regions from the Persian

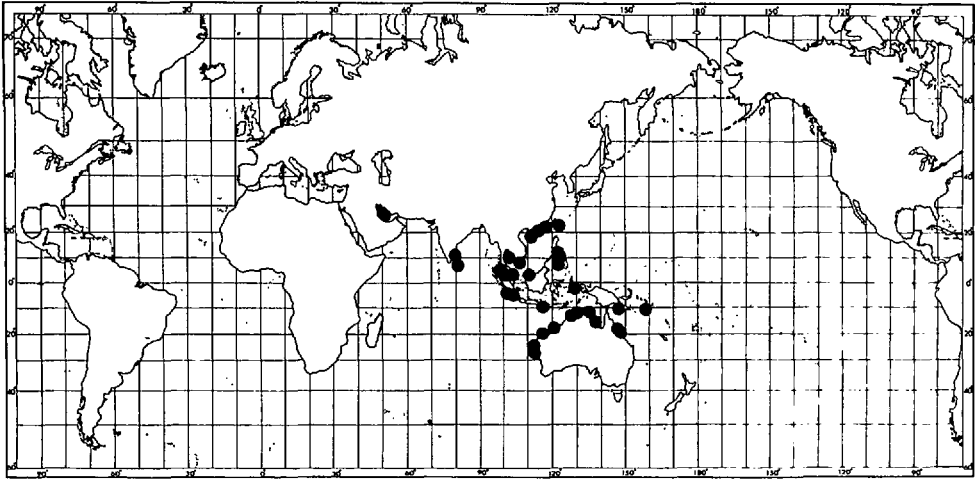


Figure 25. Distribution of *Priacanthus tayenus*.

Gulf to Great Barrier Reef of Australia and north to Taiwan; rare in East China Sea (Senta, 1977).

**Geographic Variation.**—The great ranges in scale counts given for this species are due largely to pronounced regional variation. Specimens from western portions of the range (Persian Gulf–India) have very low scale counts (LS 56–61, VSR 40–43) and modally 17 pectoral rays, while specimens from easterly portions of the range, including western and eastern Australia and northward to the South China Sea, have much higher scale counts (LS 63–73, VSR 43–50) and modally 18 pectoral rays. *Priacanthus tayenus* reportedly occurs in the interlying region (Day, 1875; Munro, 1955) but specimens are not available for examination. A single specimen from Sumatra has LS 62, VSR 43 and 17 pectoral rays. It is assumed that regional differences in meristic data are attributable to east-west clinal variation similar to that exhibited in *P. blochii* but regional distinction cannot be discounted completely. No regional trends in morphometric data are evident.

**Biological Notes.**—Occurs at depths of 20 to 200 m or more, being common at depths less than 100 m in areas of greatest abundance. Very abundant in Andaman Sea and southern South China Sea areas where it is of considerable importance in the commercial trawl fishery (Senta, 1977; Wongratana, 1982). Adults apparently occur, at least at certain times, in large schools (Senta, 1978) and in much more open bottom areas than most priacanthids, which are usually solitary near cover. Spawning season in the South China Sea is March to August (Vien, 1968). Maturing juveniles are recruited into schools at about 90–100 mm SL in June–August and reach near 200 mm SL by the end of one year after recruitment (Senta, 1978). Gonads of two out of several hundred individuals collected off Thailand, dissected by T. Wongratana (per. comm.), have gross morphology suggesting hermaphroditism; this possibility will be investigated further by Starnes and Wongratana.

**Remarks.**—External sexual dimorphism is possibly present in *P. tayenus*. Based on dissection of gonads, all six available specimens having greatly produced outer caudal rays are males whereas females in the same lot have truncate caudal fins.

However relatively large male specimens (mature?) having truncate caudal fins are present in other samples. The implications of this trait are therefore not completely understood.

The possible types of Bleeker's *P. holocentrum* and *P. schmittii* were thought to be deposited in RMNH 5554 according to a label associated with that lot. One specimen now (RMNH 30586, 185 mm SL) corresponds to the approximate length given by Bleeker (1852) for *schmittii* and it is regarded as the probable type of that species. None of the remaining specimens approach the length given by Bleeker (1849) for *holocentrum* (127 mm TL) and the type of that form may no longer be extant. The descriptions of both species clearly correspond to *P. tayenus* and Bleeker himself later (1873a) synonymized these forms with *tayenus* Richardson.

Günther (1859), in his discussion of *P. holocentrum*, mentions parenthetically a questionable name, "*Priacanthus poecilopterus*," on a Bleeker specimen from Sumatra. This name appears nowhere in Bleeker's works and is apparently an unpublished manuscript name and thus unavailable. Day (1875) discusses "*Priacanthus kawai*" of Jerdon (1851) as being an element of the Indian fauna. Inspection of Jerdon's work clearly indicates that this is a vernacular name, and though unavailable, the name evidently corresponds to *P. tayenus*.

*Material Examined*.—185 specimens, 28–221 mm SL. CHINA: ANSP 77097,1; ANSP 79552,2; BMNH 1965.18.20.50,1; 175 mm SL (probable cotype); CAS 17798,1; CAS 27665,2; CAS 54867,1; CAS 55040,1; CAS 61026,11; CAS 61253,8; CAS 60364,1; CAS GVF 1756,4; FMNH 46996,1; SU 9716,1; USNM 183158,1; USNM 56415,1; USNM 94793,1; USNM 94802,1; USNM 94809,1; USNM 131091,1. INDIA: BPBM 20510,1. INDONESIA: ANSP 27572,1; CAS 34220,1; CAS 36076,21; CAS 52633,2; CAS 52648,1; MNHN A.231,1; RMNH 317,3; RMNH 5554,5; RMNH 3058 (possible type of *Priacanthus schmittii*, 185 mm SL); SU 8083,1; USNM 264469,1; USNM 282940,1 C&S; USNM 32729,1; USNM 285025,1. MALAYSIA: MCZ 33043,1; SU 30834,3; SU 32874,1. NORTHERN TERRITORY AUSTRALIA: NTMS.10234-004,1; WAM P.14290,1; WAM P.14468,1; NTMS.10351-001,1; WAM P.29375-001,1. NEW GUINEA: KFRS F.O. 1528,1; KFRS UNREG.,1. PERSIAN GULF: BPBM 21223,1; MCZ 52758,2; USNM 265644,7; USNM 265645,1; USNM 265646,1. PHILIPPINES: ANSP 98049,2; BPBM 22160,1; CAS 32813,1; CAS 53445,5; LACM 37434-12,1; SU 21631,2; SU 27101,2; SU 27102,1; SU 27123,1; SU 39051,1; SU 39052,1; USNM 150985,1; USNM 182715,4; USNM 183157,4; USNM 183159,1; USNM 226644,1; USNM 226651,1; USNM 232030,1; USNM 232031,1; USNM 232032,6 (1 C&S); USNM 282931,1. QUEENSLAND: AMS I.15421-041,8; AMS I.2705,5; NTM 1183,1; ROM 39397,2. SOUTH CHINA SEA: BMNH 1848.3.16:141,1; USNM 282882,1. SOLOMON ISLANDS: CAS 5917,1. TAIWAN: CAS 60364,1; CAS 15623,1; FMNH 52183,1; USNM 76625,3. THAILAND: ANSP 87349,1; CAS 17671,1; CAS 55041,8; CAS GVF 2555,1. W AUSTRALIA: AMS I.20402-012,1; WAM P.5829-002,1; WAM P.25095-037,1; WAM P.4411,1; WAM P.4542,1; WAM P.8915,1. LOCALITY UNKNOWN: USNM 6521,1.

***Priacanthus zaiseræ* new species Starnes and Moyer**  
Plate IIIh; Figure 3d

*Holotype*.—USNM 284063, 212 mm SL, female, Japan, Miyake-jima, Ako, 28 m, trap net, fishermen (procured by J. T. Moyer), 2 October 1985.

*Paratypes*.—AMNH 77359, 116 mm SL, same data as holotype except 22 October 1985; AMS I.26841-001, 149 mm SL, same data as holotype except 7 November 1985; ANSP 159040, 120 mm SL, same data as AMNH 77359; BMNH 1987.6.1:4, 115 mm SL, same data as holotype except 19 October 1985; BPBM 31883, 207 mm SL, same data as holotype except 16 October 1985; CAS 60362, 235 mm SL, same data as holotype except 28 September 1985; FRLM 1892, 133 mm SL, Japan, Mie Prefecture, Shima-cho, off Katada, set net, 19 January 1979; FRLM 2470, 171 mm SL, same data as FRLM 1892 except 6 March 1980; MNHM 1987-935, 138 mm SL, same as AMS I.26841-001; NSMT P41955, 161 mm SL, Japan, Miyake-jima, Igaya, 30 m, trap net, fishermen (procured by J. Moyer), 12 April 1985; TMBS 851107-3, 139 mm SL, same as AMS I.26841-001; URM 1086, 192 mm SL, Japan, Ryukyu Islands, Senkaku, 30 December 1981; URM 8249, 178 mm SL, Japan, Okinawa, Itoman, 13 September 1983; URM 8251, 191 mm SL, same as URM 8249; USNM 284064, 132 mm

SL, same as AMS I.26841-001; USNM 284065, 2110–127 mm SL, same as holotype except 18 October 1985; USNM 289282, 230 mm SL, Philippine Islands, Siayan Island, Batanes, fisherman (procured by G. D. Johnson, W. Smith-Vaniz), 25 April 1987.

**Diagnosis.**—A medium-sized (to perhaps 250 mm SL) member of *Priacanthus hamrur-blochii* species group characterized by obsolescent preopercular spines in adults and black basal spot on pelvic fins. Distinguished from all members of this group by having bright yellow pectoral fins in life. Distinguished from the *hamrur* subgroup (*arenatus*, *hamrur*, *meeki*, *prolixus*) in not having a crescentic caudal fin nor increased numbers of soft dorsal- and anal-fin rays (modally 13 and 14 vs. 14 and 15). Distinguished from all *blochii* subgroup members (*alalaua*, *blochii*, *nasca*, *sagittarius*) by thinner, more tapered gill rakers as in *P. hamrur* (Fig. 18b), and higher gill raker counts (25–28 vs. 17–23).

**Description.**—Based on 13 specimens, dorsal-fin rays X, 13; anal-fin rays III, 14 (13–14); pectoral-fin rays 19 (18–19); scales in lateral series 81–89 (83.6); lateral-line scales 71–76 (73.2); vertical scale rows 51–57 (54.1), 9–11 above lateral-line, 40–45 below; total gill rakers on first arch 25–28 (26.0), 19–22 on lower limb, 5–6 on upper.

General profile evident in Plate IIIh. Largest known specimen 235 mm SL. Caudal truncate to very slightly emarginate. Soft dorsal and anal fins broadly rounded and of moderate length, subequal or slightly exceeding eye diameter. Pectoral fins of moderate length and broadly pointed, subequal in length to pelvic spines. Pelvic fins usually reaching second anal-fin spine. Preopercular spine reduced to a slight prominence in larger adults. Lacrymal and second infraorbital with fine serrations as in *P. sagittarius* (Fig. 5a). Extrinsic swimbladder muscles situated as in *P. hamrur* (Fig. 10b). Midlateral scales similar in configuration to *P. alalaua* but with fewer (30–40) spinules (Fig. 3d).

Body proportions are based on 10 specimens 133–235 mm SL. BD 373–409 (396), BW 163–198 (173), CPL 148–164 (156), CPD 077–089 (083), HL 300–335 (321), HD 337–369 (346), HW 170–204 (186), ORB 152–173 (160), IO 076–087 (082), SN 078–101 (087), JW 194–213 (202), D1L 139–164 (147), D2L 161–195 (175), AL 151–179 (163), P1L 170–193 (179), P2L 254–278 (265). Ontogenetic variation does not appear to be great in this species. There is definite negative allometry in caudal peduncle length which decreases proportionately with maturity. The largest specimen is abruptly more robust than those slightly smaller (reflected in BW) which, based on trends in other species of the genus, is probably true of all larger specimens. Variation in other distances does not appear to correlate appreciably with ontogeny.

Color in life (based on transparencies of fresh-killed specimens) bright red on head, iris of eye, body, and dorsal, anal and caudal fins. Head and body sometimes with silvery blotches. Interior of mouth bright orange, especially on palatines and inner cheek area. Pectoral fins bright yellow; pelvic fins with red rays, dusky membranes and a black basal spot on dorsal surface; dorsal fins, anal and caudal fins with a dusky fringe. Pelagic juvenile pigmentation patterns are unknown.

**Distribution.**—Definitely recorded only from localities (Fig. 19) in southern Japan and the northern Philippine Islands, including the Ryukyus, Tosa Bay (Okamura, 1985), off Katada (Kimura and Suzuki, 1980) the Izu Archipelago, and Batanes. Okamura (1985) also reports from the “Okinawa Trough” region without precise locality information. Probable specimens of *zaiserae* have also been observed by Moyer in markets at Cebu, Negros, Philippines. All records thus far are from the northwestern margin of the Philippine Plate.



*Biological Notes.* — All specimens for which habitat information is available were netted in rocky bottom areas at depths of about 30 m. Okamura (1985) reports a maximum depth of 320 m. Large female specimens (over 200 mm SL) collected during December appeared to be approaching spawning condition based on dissection of gonads; smaller specimens (less than 160 mm SL) appeared to have immature gonads.

*Remarks.* — This form has been recognized by several Japanese authors as a probable undescribed species (Masuda et al., 1975; 1984, "Sp. 2"; Kimura and Suzuki, 1980, "Sp. Type 1"; Okamura, 1985, "Sp. A"). It had also been under study recently by the second author of this description (J. T. Moyer), as well as being independently sought after by the first. We therefore have collaborated to describe it within the present work for the sake of completeness.

*Etymology.* — Named for Martha J. Zaiser, formerly of Tanaka Memorial Biological Station, Miyake-jima, Japan; the second author especially wishes to recognize her valuable contributions to the knowledge of the marine biogeography of the Izu Islands.

#### PHYLOGENETIC ANALYSIS

The phylogenetic tree depicted in Figure 26 represents the hypothesis of relationships for the Priacanthidae arrived at by a hand process of Hennigian argumentation. Comparisons to a generalized outgroup composed of perciform and beryciform fishes together with ontogenetic information were used to estimate character polarity. The hypothesis was later corroborated in a computer cladistic analysis using the global branch swapping option of D. L. Swofford's PAUP (Phylogenetic Analysis Using Parsimony) program. Trees of similar basic topology (varying only with respect to alternate resolutions of polytomys) were generated having lengths of 47 steps and a consistency index (a measure with an inverse relationship to the degree of homoplasy present) of 0.872. The following character analysis refers to the numbered synapomorphies on the cladogram in Figure 26. Pertinent anatomical features have been further described in the familial and generic accounts. Characters 1–13 support a hypothesis of monophyly for Priacanthidae.

1) Modified spiny scales. Priacanthids have bony spines emanating directly from scales rather than borne on separate platelets as in true ctenoid scales. A few outgroup families also have spiny scales, including the percoid families Pomacanthidae and Scatophagidae and all beryciform families. However none possesses the extreme scale modifications described for Priacanthidae exemplified by the mandibular scale shown in Figure 1.

2) Form of first epibranchial and lack of interarcual cartilage. The flanged T-shaped first epibranchial of priacanthids and its associated ligamenture (Fig. 5b) are unique among groups examined. Some other groups (i.e., ambassids, some chaetodontids, pomacanthids, scorpioninines, scatophagids) have a more or less posteriorly directed uncinat process but all with the exception of scatophagids have an interarcual cartilage (Travers, 1981) connecting this element to the second pharyngobranchial. In priacanthids the strengthened association between the pharyngobranchials typically afforded by an interarcual cartilage appears to be supplanted by the ligamentous connection.

3) Single postcleithrum. This element is a single bone and comparatively very slender in priacanthids not having separate dorsal and ventral components as in

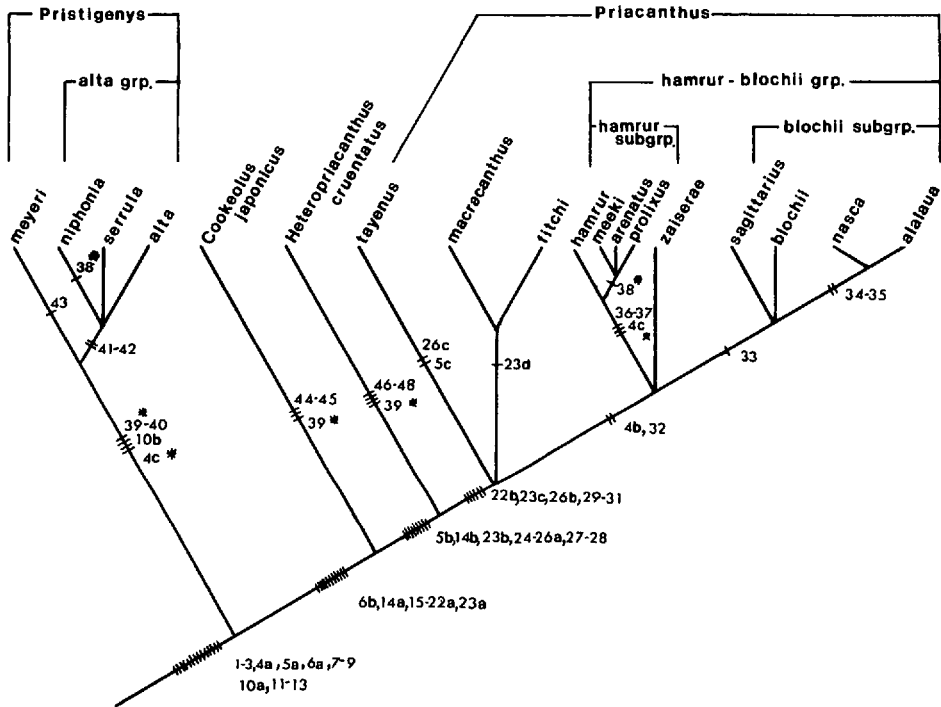


Figure 26. Cladogram depicting hypothesized relationships among priacanthids. Numbered synapomorphies correspond to those in "Phylogenetic Analysis." Hypothesized homoplasous characters are denoted by asterisks.

outgroup genera. It is either singular throughout development or fuses very early (pretransformation). Postflexion larvae had this element insufficiently developed or stained to detect whether separate chondrification centers were present.

4a-c) Preopercular spine. Priacanthids retain a large spine at the posteroventral angle of the preopercle postransformationally. Larvae of several outgroup families, including acropomatids, apogonids and epigonids, caesionids, carangids, cepolids, chaetodontids, lethrinids, lutjanids, lobotids, malacanthids, scombroptids and serranids possess spines of various lengths at this location (Leis and Rennis, 1983; Johnson, 1984). But all except the serranid *Nippon* lose it following transformation and its pedomorphic retention in priacanthids is therefore considered derived (4a). Other families (i.e., pomacanthids, centropomids) possess preopercular spines as adults but develop them postransformationally. In larger specimens (over 100 mm SL or so) of *Priacanthus zaiserae*, *P. sagittarius*, *P. blochii*, *P. nasca* and *P. alalaua* the spine becomes much reduced (4b) and becomes completely obsolescent in adults of *Priacanthus hamrur*, *P. arenatus*, *P. meeki*, *P. proluxus* and all species of the genus *Pristigenys* (4c). By overall parsimony, this secondary process of terminal deletion is regarded as a transformational series in the phyletic line including *Priacanthus* with a homoplasous loss in *Pristigenys*.

5a-c) Serrate infraorbital bones. The prevalent condition in outgroup members is to have the lacrymal and other anterior infraorbital bones smooth or finely serrate. The spiny armature of these bones in priacanthids (Fig. 5a) is considered derived (5a). These spines are present in small juveniles of all priacanthids but become secondarily reduced to fine serrations in *Heteropriacanthus* and all *Pria-*

*canthus* except *P. tayenus*, a condition considered derived within the family (5b). By overall parsimony the large spines possessed by *P. tayenus* are considered a reversal to the primitive state for the family (5c).

6a, b) Reduction in predorsal elements. The primitive complement of predorsal bones in percoids is believed to be three (Fraser, 1972; Johnson, 1984). The reduction to one element in *Pristigenys* (Fig. 7a) is considered derived (6a) and the loss of all elements in *Cookeolus*, *Heteropriacanthus* and *Priacanthus* (Fig. 7b, c) further derived (6b).

7) Reduction in vertebral number. Only one other percoid group, scatophagids, possesses only 23 vertebrae, a reduction from the presumed plesiomorphic range of 24–27 (Gosline, 1968; Johnson, 1984).

8) Reduction in caudal ray number. Sixteen (8+8) principal caudal rays, reduced from the presumably primitive complement of 9+8, occur among percoids only in priacanthids, acanthoclinids and scatophagids (Johnson, 1984). Absence of a procurent spur accompanies all such reductions but is not restricted thereto, occurring widely among beryciform and perciform families (Johnson, 1975), limiting assessment of its utility as an additional, possibly related, character.

9) Loss of intercalar (opisthotic) bone. This superficial bone, which usually caps the common joint of the exoccipital, prootic and pterotic bones, sometimes forming articulation of the posttemporal, is difficult to detect but appeared to be present in several outgroup members examined. The extent of absences throughout all outgroup families is unclear and should be the subject of a rigorous study beyond the scope of this work. The loss of this bone in priacanthids is provisionally considered derived.

10a, b) Fin ray spinules. The spines and soft rays of priacanthids possess numerous well developed spinules (see family description) including biserial rows on the soft dorsal and anal rays. Among the outgroup, spinules were found on the fin elements only in the beryciform family Trachichthyidae which has uniserial rows of weak spines on the soft rays of the median fins. The presence in priacanthids of these structures appears then clearly derived (10a) with the ontogenetic loss of spinules from the dorsal spines of larger specimens of *Pristigenys* being a secondary derivation (10b).

11) Scales on branchiostegals. Scales rarely occur on the branchiostegal rays of fishes but are present in priacanthids. They were not present in any of the outgroup genera examined but, beyond that, are known to the author to be present in the percoid subgenus *Psychromaster* (genus *Etheostoma*).

12) Adnate pelvic fins. The extensive membranous connection between pelvic fins and the belly of priacanthids does not occur in other percoid or beryciform out group members examined, but, beyond that group, occurs in some siganids.

13) Type of tapida lucidum. Nicol et al. (1973) surveyed tapida lucida of the eyes of a broad taxonomic selection of fish groups and found that of *Priacanthus* to be unique, a highly differentiated chorioidal reflective stratum backing the retina lined with flat guanine crystals similar to a type found elsewhere only in sharks and sturgeons. My examination revealed the same type of tapida throughout other priacanthid genera but dissection of other large-eyed fishes not investigated by Nicol et al. (i.e., the percoids *Glaucosoma* and *Pempheris* and several beryciform genera) revealed a very different tapida not well differentiated from other strata, similar to the lipid type described by Nicol et al.

14a, b) Reduction first neural spine. The first neural processes in priacanthids are autogenous and fuse to the foramen magnum in larger specimens. In *Pristigenys* the processes fuse dorsomedially to form a spine (Fig. 7a), the general condition found in outgroup members. In *Cookeolus* the processes are reduced and not fused

medially (Fig. 7b) (14a) and in *Heteropriacanthus* and *Priacanthus* are further reduced to mere vestiges (Fig. 7c) (14b).

15) Relationship of haemal spines and basal anal pterygiophores. In most deep-bodied fishes reinforcement is formed between the axial skeleton and anal fin, typically by elongation of the anterior basal anal pterygiophores which often intergroove with or bind with the haemal spines. That situation occurs in *Pristigenys* (Fig. 8a) but in the three remaining genera of priacanthids this reinforcement is augmented by much longer and more massive anterior haemal spines intergrooved with and tightly bound to the basal pterygiophores (Fig. 8b). Among the outgroups, a similar condition was found only in the freshwater percoid family Centrarchidae in which the bones involved are much less massive.

16) Enlarged pelvic girdle flange. In outgroup families plus *Pristigenys* the pelvic bones bear narrow flanges ventrally; these flanges are considerably expanded in *Cookeolus* and other priacanthid genera (Fig. 5a).

17) Broad suturing of ceratohyal bones. Though variable, the prevalent condition among outgroup genera is to have the anterior and posterior ceratohyal bones joined by cartilage only or narrowly bound by sutures as in *Pristigenys*. In *Cookeolus*, *Heteropriacanthus* and *Priacanthus* these bones are joined by broad sutures (Fig. 5d).

18) Restricted opening of preopercular sensory canal. In the majority of outgroup genera examined the vertical arm of this canal is primarily open posteriorly; to a lesser degree the ventral arm is also open being overlain by a shelf as in *Pristigenys*. It has restricted openings and is somewhat more enclosed by overlying bones in a few groups (i.e., scatophagids, *Drepane*). Restricted apertures in the three remaining genera of priacanthids are thus considered derived.

19) Median crest of frontals. The configuration of the medial joint of frontal bones varies widely among outgroup members but the generalized condition appears to be a broad median ridge, the condition present in *Pristigenys*. The high sagittal crest developed at the joint of these bones in larger specimens of *Cookeolus*, *Heteropriacanthus* and *Priacanthus* is considered derived.

20) Loss of epipleural rib. *Pristigenys* has six epipleurals (associated with vertebrae 3–8) and outgroup members have six or more. The loss of the epipleural associated with vertebra 8 in the three remaining genera of priacanthids is apparently derived.

21) Gonad configuration. The generalized condition among outgroup members and *Pristigenys* is to have the gonads elongate and tubular. Those of the three other priacanthid genera are broadly triangular, a presumed synapomorphic condition.

22a, b) Condition of scale circuli. Scanning electron microscope photography of body scales of priacanthids, several outgroup genera, and a variety of fishes from several orders revealed that the great majority possess denticulate structures of various kinds on the primary ridges or circuli on the anterior field. These structures were termed “beads” by McCully (1961),<sup>2</sup> “teeth” by DeLamater and Courtenay (1974) and “lepidonts” by Hollander (1986). The authors supposed that the structures might prove to have systematic significance. In priacanthids three very different conditions exist, remarkable considering the limited intrafamilial variation in other groups examined. These conditions would appear to form a transition series from the plesiomorphic state of *Pristigenys* (Fig. 4a), to the

<sup>2</sup> McCully, H. H. 1961. The comparative anatomy of the scales of the serranid fishes. Unpub. Dissert. Stanford Univ.

corrugate condition of *Cookeolus* and *Heteropriacanthus* (Fig. 4b, c) (22a), to the essentially smooth ridges of *Priacanthus* (Fig. 4d) (22b).

23a-d) Modification of posterior scale field. The common condition among outgroup members is to have a basically flat scale bearing ctenii on separate platelets along the posterior margin and on the surface of the apical (posterior) field or, in the case of a few groups having non-ctenoid scales (see Character 1), spines situated on the posterior margin as in *Pristigenys* (Fig. 2a-d). In the remaining priacanthid genera the apical field has become elevated, supported by a separate prominence or flange, and bears an array of spination configurations. This variation is interpreted as a transitional series as follows: in *Cookeolus* (Fig. 2h) the field is slightly elevated, supported by a slight medial prominence, and bears spines along the margin (23a); in *Heteropriacanthus* the field is considerably elevated and supported by a fully developed "footer flange" (Fig. 2g) and bears spines only along the margin (23b); in *Priacanthus*, the basic configuration is as in *Heteropriacanthus* but spines have developed on the surface of the field (Figs. 2e, f, 3a, b, d-g) (23c). The extremely broad and spiny apical field configurations uniquely shared by *P. fitchi* and *P. macracanthus* (Fig. 3e, g) are considered further derived, possibly by terminal addition or substitution (23d). Juveniles of *P. sagittarius* and *P. tayenus* have scales appearing basically as in other *Priacanthus* species (Fig. 3f) but the apical field undergoes a remarkable ontogenetic recession with the terminal condition being a narrow pointed or rounded spineless flange (Fig. 3c, h). These recessions are interpreted as autapomorphic derivations based on the very different terminal configurations of the apical flanges.

24) Modification of haemal spines. In *Pristigenys*, *Cookeolus*, and the vast majority of outgroup genera, haemal spines emanate from the anterior portion of the vertebral centra and the posterior zygapophyses project posteroventrally (Fig. 8a) (except occasionally the ninth caudal vertebra of *Cookeolus*). In *Heteropriacanthus* and *Priacanthus* haemal spines emanate centrally and are fused with the zygopophyses to form inferior foramina through which lateral arteries pass (Fig. 8b). In percoids a similar condition was found only in ehippids and scatophagids. Beyond the outgroup, such fusions occur in some scombroids (e.g., *Euthynnus*).

25) Posterior projections of swimbladder. The primitive swimbladder of percoids appears to be a simple capsular configuration as in *Pristigenys* and *Cookeolus* (Fig. 9a) with elaborations being specialized. The posterior projections in *Heteropriacanthus* and *Priacanthus* (Fig. 9b, c), which have apparently developed independently in some other groups, particularly deep-bodied ones, are considered apomorphic.

26a-c) Presence of extrinsic swimbladder muscle (23a). Swimbladder muscles to enhance sound production have evolved in several fish groups, including, among groups considered here, holocentrids, sciaenids (Tavolga, 1971), and pempherids and teraponids (Vari, 1978). These muscles either partially surround the bladder (sciaenids) or extend from anterior ribs and connective tissue associated with the bladder to the occipital region of the head. The short muscles described herein and in part by Salmon and Winn (1966) for *Heteropriacanthus* and *Priacanthus* which extend forward from the first pleural rib and insert directly on the anterior region of the swimbladder are apparently of a unique configuration. There are three variations of this basic configuration. In *Heteropriacanthus* the muscles are present (26a) and extend forward from their origin on the first rib to insert medially on and partially cap the anterior of the bladder (Fig. 10a). This arrangement is considered least derived within the family as the swimbladder of *Heteropriacanthus* retains the primitive truncate anterior configuration (see Character

29 below). In *Priacanthus*, with the evolution of the specialized anterior projections of the swimbladder, these muscles have apparently been displaced ventrolaterally (Fig. 10b) (26b). In *Priacanthus tayenus*, these muscles have become further displaced and connect beneath the swimbladder by means of a broad ligamentous band which is narrowly connected to the swimbladder medially (Fig. 10c) (26c).

27) Two posterior projections of interopercle. In *Heteropriacanthus* and *Priacanthus* the posterior margin of the interopercle is deeply notched (often covered by very thin sheet of bone in *P. fitchi*), thus creating two posterior projections, a presumably derived condition. In *Pristigenys* and *Cookeolus* and outgroup genera, this bone is broadly pointed to truncate posteriorly.

28) Anterior projections on scales. In the majority of beryciform and perciform outgroup genera investigated the body scales have truncate to slightly scalloped anterior margins as in *Pristigenys* and *Cookeolus* (Fig. 2a–c, h). The very prominent anterior interradiar projections of *Heteropriacanthus* and *Priacanthus* scales (Figs. 2e–g, 3a–h) are thus considered derived.

29) Anterior swimbladder projections. *Pristigenys*, *Cookeolus* and *Heteropriacanthus* have anteriorly truncated swimbladders (Fig. 9a, b) which do not penetrate the anterior wall of the body cavity, as in the vast majority of outgroup members. The specialized anterior projections of *Priacanthus* swimbladders (Fig. 9c), which extend from the body cavity to communicate with the skull, are thus derived.

30) Sacculus fossae of skull. The posteroventral aspect of the skull of *Priacanthus*, including the prootic, exoccipital and basioccipital bones, is greatly modified to form a deep fossa over the sacculus in which the anterior swimbladder projection resides, thus being brought into close communication with the otoliths (Fig. 6b). This condition contrasts with that in other priacanthids (Fig. 6a) and all outgroup genera and is considered derived.

31) Enlarged carotid foramina. These apertures are considerably enlarged in *Priacanthus* (Fig. 6b) compared to those of other priacanthid genera (Fig. 6a) or outgroup members examined.

32) Axial pelvic blotch. The distinctive basal blotch on dorsal surface of the pelvic fin shared by all species of *Priacanthus* included in the *hamrur-blochii* species group in Figure 26 is absent in outgroups.

With the sister group relationships established thus far by extrafamilial outgroup comparison (characters 1–32), characters within the *P. hamrur-blochii* species group will be polarized according to conditions present in these intrafamilial sister groups (functional outgroup), as the type of characters used are too variable in extrafamilial groups to be evaluated.

33) Gill raker number and morphology. Relative to all other priacanthid species except *Priacanthus tayenus* the gill raker counts of *Priacanthus sagittarius*, *blochii*, *alalaua* and *nasca* are reduced (range of modes 20–22 vs. 23–26 in 10 species; *Priacanthus arenatus* and *P. meeki* are high at 30–31). The gill rakers of these species are relatively thick and rounded and less tapering with spinules distributed over nearly half of the circumference on the medial aspect (Fig. 18a). Gill rakers of all other species of *Priacanthus*, including *tayenus*, as well as sister genera, are more tapered, flatter and have the spinules concentrated near the medial edge (Fig. 18b). The shared raker morphology and lower counts of *P. sagittarius* and the others is regarded as derived from the presumably primitive modal range of 23–26 with the reduced count (modally 22) in *P. tayenus*, which has non-derived morphology, regarded as homoplasious.

34) Elongate pectoral fins. All species of *Priacanthus* and the sister genus *Het-*

*eropriacanthus* have short (averaging 0.18 SL or less), broadly pointed pectoral fins, except *P. fitchi*, many Indonesian specimens of *P. macracanthus*, *P. alalaua* and *P. nasca*. The much longer (averaging near .210 SL), more pointed pectoral fins shared by *P. alalaua* and *P. nasca* are considered derived within the *blochii* subgroup and, by overall parsimony, homoplasious with those of *P. fitchi* and *P. macracanthus*.

35) Reduced upper jaw length. The gape, as evidenced by upper jaw length (.150–.171 of SL), is notably reduced in *P. alalaua* and *P. nasca* relative to other members of the *blochii* subgroup and all other priacanthids which have upper jaw lengths ranging above .180 of SL. This reduction is thus considered apomorphic.

36) Crescentic caudal fin. The generalized caudal fin shape for sister genera of priacanthids is rounded to truncate. The crescentic fin shared by *P. hamrur*, *P. arenatus*, *P. meeki*, and *P. proluxus* is thus considered derived. Some individuals (males?) of *Priacanthus tayenus* have the outer caudal rays produced to filamentous proportions, resulting in an extremely lunate configuration. This modification appears non-homologous to the crescentic fins of the *hamrur* subgroup.

37) Increased median fin rays. The soft dorsal-fin ray counts for *Cookeolus* and *Heteropriacanthus* are modally 13 and anal-fin rays 13 and 14 respectively. All members of *Priacanthus* have similar complements (or fewer) except *P. hamrur*, *P. arenatus*, *P. meeki*, and *P. proluxus* which usually have 14 or more soft dorsal rays and 15 or more soft anal rays, a presumably derived condition.

38) Increased gill raker counts. *P. arenatus*, *P. meeki*, and *P. proluxus* share increased gill raker counts (modally 29 to 31) above the presumably primitive range for priacanthids of 23–26 (see character 33 above). *Pristigenys niphonia* has modally 28, here construed to be independently derived.

With the analyses of the phyletic line culminating in *Priacanthus* species completed, character analyses for other priacanthid genera will return to a primarily extrafamilial outgroup comparison approach.

39) Reduction in procurent rays. *Pristigenys* has 3 procurent rays, *Cookeolus* and *Heteropriacanthus* 4, and *Priacanthus* 5. Most outgroup members have more to considerably more than 5 rays. Within the context of the arrived at phylogeny, the reductions in *Pristigenys*, *Cookeolus* and *Heteropriacanthus* must be considered independent derivations.

40) Black marginal fin bands. The discrete black marginal band occurring on the soft dorsal and anal fins and caudal fin of *Pristigenys* species are unique among the family and outgroups.

41) Reduction in median fin rays. *Pristigenys alta*, *P. niphonia* and *P. serrula* have 11 soft dorsal-fin rays and 10 soft anal-fin rays (vs. 12 and 11 respectively in *P. meyeri*). Based on comparison with all other priacanthids whose range of modes is 12–14 for dorsal rays and 13–15 for anal rays, this reduction is presumed derived.

42) Color pattern. The color pattern of broad bands separated by narrow bars shared by *P. alta*, *niphonia* and *serrula* is unique among the family and outgroups.

43) Enlarged scale spines. In outgroup genera having spinous scales the common condition is to have about 25–40 small spines projecting from the posterior margin similar to those found on scales of *P. alta*, *niphonia* and *serrula* (Fig. 2a, b). The reduced numbers (8–20) of larger spines found in *P. meyeri* (Fig. 2c) are thus considered autapomorphic.

44) Supracleithral spine. In all priacanthid genera except *Cookeolus* the supra-clithrum is a simple elongate blade-like bone while that of *Cookeolus* bears a posteriorly directed spine dorsally that becomes a broad process in large adults

(Fig. 5g). In outgroup genera this bone is usually relatively simple and elongate and often bears a portion of the lateralis system dorsally (not so in priacanthids). The spined condition of *Cookeolus* is thus autapomorphic.

45) Elongate pelvic fins. The extremely long pelvic fins possessed by juveniles and smaller adults of *Cookeolus*, which ontogenetically recede, are unique among the family and outgroups.

46) Flanges on pleural ribs. *Heteropriacanthus* alone possesses expanded flanges on the posterior pleural ribs compared to the relatively narrow flanges on ribs of other genera (Fig. 5f) which is the prevalent condition in outgroups.

47) Absence of scales on posterior preopercle. *Heteropriacanthus* uniquely lacks scales on the preopercle posterior to the sensory canal and has generally deeper striations in this region than other genera.

48) Specks in membranes of median fins. *Heteropriacanthus* uniquely possesses elliptical specks in the membranes of dorsal, anal and caudal fins.

### Discussion

Priacanthids are a phenetically "obvious" group, particularly because of the large eyes, deep compressed body shape, rough scalation and spination, and predominantly reddish coloration. However such characters as eye size, body shape and general coloration are not assessable in a cladistic analysis when utilizing a broad outgroup approach because of wide occurrence in varied groups. They are possibly as uniquely derived in priacanthids as the initially less obvious but more unique characters (1-13) analyzed above which are hypothesized to corroborate the monophyly of priacanthids.

It would appear that several of the internal modifications discussed above are reductive ones perhaps associated with the evolution of an extremely large orbit and possibly some foreshortening of the body. The reduction in vertebrae, loss of predorsal bones, reduction of neural processes and possibly loss of the intercaler bones may be a product of evolutionary compression of the nuchal region. The scales too have been a particularly dynamic area of modification and have provided much information for cladistic analysis. The evolutionary scheme for scales, as well as fin-ray spination, seems to be one of providing maximum abrasiveness, perhaps linked to some protective behavior. A third interesting suite of characters is found among priacanthids in comparative swimbladder morphology as well as the presence or absence of and morphology of swimbladder muscles. Several varied adaptations for the production, and possibly the reception, of sound have evolved within the group and these functions must be important components of their behavioral repertoire.

The hypothesis of overall relationships depicted in Figure 26 is well corroborated by apparent specializations, especially at the generic level. As is typically the case in cladistic analyses, relationships at the species level are much less corroborated. Overall, hypothesized homoplasy is not very pervasive as indicated by the relatively high consistency index of 0.872 generated by the PAUP computer cladistic analysis.

With the data at hand, it was not possible to further refine hypotheses of priacanthid relationships at the species level. For instance, in the genus *Pristigenys*, the three species contained within the *alta* species group in Figure 26 are phenetically highly similar, differing only in meristics and slightly in some aspects of shape. Considering the species together, the data for these attributes form continua which do not lend themselves to outgroup comparison and/or are conflicting. Thus a branching sequence cannot be resolved between them. By a similar token, in the *Priacanthus blochii* subgroup, *P. blochii*, *P. alalaua* and *nasca* are phenet-



ically similar such that they had to be carefully compared with regard to their distinctiveness, particularly in the case of *blochii* and *nasca*. Though a sister species relationship between *alalaua* and *nasca* is corroborated, a close relationship of these species to *blochii* relative to the fourth member of the subgroup, *sagittarius*, cannot be demonstrated cladistically. Morphological features which vary among such closely related species and thus offer potential grouping characters (i.e., median fin shapes, scale size and others) are too labile in sister groups for evaluation. More extensive detailed data on such attributes as life coloration may have afforded better resolution.

With regard to previous hypotheses of relationships for priacanthids, Lee (1984) analysed results of electrophoretic studies of a single muscle protein in six species from Taiwan: *Pristigenys niphonia*, *Cookeolus japonicus*, *Heteropriacanthus cruentatus*, *Priacanthus sagittarius* (as "*P. blochii*"), *P. hamrur* and *P. macracanthus*. The electrophoretic data were subjected to a UPGMA cluster analysis (Sneath and Sokal, 1973), a phenetic method of assessing relationships. Lee's results are, in part, congruent with the relationships hypothesized herein (Fig. 26) since *Pristigenys* was deemed the sister group to the other considered priacanthids. However Lee's tree is completely incongruent in higher branches, with *Cookeolus* hypothesized to be the sister species to *Heteropriacanthus* + *P. sagittarius* and the three of these collectively the sister group to *P. hamrur* + *P. macracanthus*. Within the context of the phylogeny hypothesized herein, it would be necessary to reverse the polarity of many morphological characters estimated by outgroup comparison to arrive at Lee's configuration. His results are doubtless impaired by an incomplete data set, as 11 of 18 species are missing from the analysis, an understandable shortcoming considering the difficulties in acquiring frozen specimens from diverse regions of the world. The distinction between plesiomorphic and apomorphic alleles was incompletely established and, had it been, would not have been instrumental in the phenetic analysis utilized.

Shao and Chang (1985) drew phylogenetic inferences based on morphometric analyses performed on the same six species as Lee (1984) above, plus *Pristigenys meyeri* (as "*P. multifasciata*") and *Priacanthus tayenus*. One of their maximum consensus trees is partially congruent with the phylogeny presented herein in considering *Pristigenys* and *Cookeolus* as sequential sister groups to a lineage consisting of *Priacanthus* and *Heteropriacanthus*. Their placement of *Heteropriacanthus cruentatus* within the midst of this latter grouping, however, is clearly the result of misleading external similarity in a species whose distinctiveness and phylogenetically useful characters are primarily internal (see "Remarks" under genus description of *Heteropriacanthus*). If *H. cruentatus* is removed from the "*Priacanthus*" grouping, then their suggested relationships among the remaining members is, as far as determined, generally congruent although not as inclusive as the phylogeny presented herein.

Only a single reference to possible extrafamilial relationships of priacanthids was encountered in the literature, that of Jordan and Evermann (1896) who suggested a close relationship with the superficially similar pempherids. Comparative anatomical studies revealed no clearly shared derivations suggesting such a relationship. Tominaga (1968) arrived at the same conclusion in his study of Pempheridae.

No hypothesis of extrafamilial relationships is forthcoming from this study. Comparative morphological studies with the many families constituting the outgroups in the course of character analysis failed to reveal features which were likely to be shared derived. Several of the characters corroborating the monophyly of priacanthids were unique conditions while others were of scattered occurrence

throughout the outgroup. Most falling in the latter category were reductive characters resulting in complete loss of structures thus negating any evaluation of homology through comparative examination of morphology. For instance priacanthids share more "uncommon" morphological conditions with scatophagids than any other outgroup member, including reduction of predorsal elements and forward shift of fin, reduction of caudal rays and loss of procurent spur, lowest vertebral counts among percoids (exclusively shared), spiny scale type, modified haemal spines having lateral foramina (present only in two genera of priacanthids), and loss of interarcual cartilage. All but the latter three of these characters are reductive losses (interarcual cartilage loss probably an evolutionary substitution). While both families have spiny rather than ctenoid scales, the basic morphologies are very different and probably non-homologous. If one subscribes to the view held by many that the primitive sister group(s) to percoids (via monophyly or polyphyly) lies among the beryciform fishes, which have spiny scales, then this scale type may be plesiomorphous among percoid families even though they are vastly outnumbered by ctenoid scales among these groups. Thus it is easy to dismiss most all shared conditions between priacanthids and scatophagids as probably homoplasious reductions linked to body foreshortening or, in the case of scale type, possibly plesiomorphic. Scatophagids, which are phenetically highly dissimilar to priacanthids and have traditionally been included among the so-called "Squamipinnes" fishes, have been hypothesized to be the sister group to acanthuroid fishes by Mok and Shen (1983) and in a soon to be published work by J. T. Tyler et al. (pers. comm., G. D. Johnson). Aside from losses, priacanthids share none of the characters hypothesized by Tyler et al. to define the phyletic lineage including ehippids plus scatophagids plus acanthuroids, such as distinctively formed interopercle, articular-dentary configuration, non-protrusible premaxilla and other characters.

This study contributes little to facilitate hypotheses of cladogenic order for the largely unfathomed relationships of "percoid" fishes except to provide data for those who continue to pursue formulation of such hypotheses. It is possible that infinite inclusion of additional outgroup members may eventually reveal a candidate sister group or that, just as possible, relationships may be forever obscured by extinctions.

#### BIOGEOGRAPHY

As noted in the generic account, fossil specimens of *Pristigenys* are known from the Eocene and Oligocene of southern Europe and the Middle East (Sorbini, 1983) indicating that this genus, if not the entire family, was distributed in the Tethyan Seaway. Though they are absent from portions of that region today (Mediterranean), there is ample evidence to suggest that many forms may have had a nearly circumtropical distribution. Several fossils ascribed to the genus *Priacanthus* have also in fact been described from Miocene deposits in Europe but the status of these has not been determined relative to the osteology of Recent forms, a topic for future study. *Pristigenys* and *Priacanthus* are hypothesized herein to be at phyletic extremes (Fig. 26). Therefore, an additional implication of these fossils is that, if those ascribed to *Priacanthus* have been classified correctly, evolution of all priacanthid genera occurred prior to the Miocene, if not long before.

With regard to species-level biogeographic implications, three clades within the phylogeny depicted in Figure 26 are sufficiently resolved to permit limited analyses. That of the *Priacanthus blochii* subgroup, while not fully resolved, still offers area relationship information. Based on distributions of the involved taxa (Figs.

19, 24), a closer area relationship is indicated between Easter Island (*P. nasca*) and the Hawaiian Islands-eastern Pacific area (*P. alalaua*) than either area has with the Indo-West Pacific region where both possible sister species (*P. blochii* or *sagittarius*) to the *alalaua-nasca* species pair occur. This hypothesis is partially in line with the general view expressed by Rotondo et al. (1981) and Springer (1982) that many Hawaiian species have their nearest relatives in southeastern Oceania but is complicated by the fact that *P. alalaua* also occurs in the eastern Pacific. Thus these populations are the true "nearest relatives" of the Hawaiian populations but may be a product of post-evolutionary dispersal. A second clade, that of the *Priacanthus hamrur* subgroup (Fig. 26), has among its members a Hawaiian species, *P. meeki*. Assuming that *P. prolixus* is confined to the western Indian Ocean or Indo-West Pacific (Fig. 20), then the nearest probable relatives of *meeki* lie to the east of Hawaii in the Galapagos area (see "Remarks" under *P. meeki* account) and Atlantic, beyond the realm of Oceania. This hypothesized area relationship is thus at variance with the view of Rotondo et al. and Springer.

Speciation events spanning the East Pacific Rise region are implied for both the *P. blochii* and *P. hamrur* subgroup clades. Rotondo et al. (1981) and Springer (1982) discuss the "island integration" theory wherein islands born near the East Pacific Rise may have been transported northwestward, along with their faunas, with movement of the Pacific Plate into the Hawaiian volcanic region, thus effecting isolation from faunas left behind to the east and resulting in Hawaiian endemism. Though these authors did not hypothesize a precise area of origin for these islands, the west-northwestward course and rate of movement of the Plate since the late Eocene (Duncan and Clague, 1985) would have indeed swept the northern end of the Line Island chain through the vicinity of the Hawaiian "hot spot" 20–25 million years ago near the beginning of the Miocene. This would have afforded the most likely opportunity for faunal integration. However, such a scenario would predict that nearest relatives to Hawaiian species would occur in the Line Islands to the south. This is not the case in priacanthids and thus such a hypothesis is not corroborated. An alternate hypothesis is that gene flow to Hawaiian populations of progenitoral species may have been facilitated via pelagic transport in former, somewhat altered, eddy patterns of equatorial currents, effectively sustaining them for a time as one with more easterly (eastern Oceania or eastern Pacific) populations. These currents eventually assumed or resumed present configuration, isolating Hawaiian populations and facilitating speciation. This may have occurred after the northern Line Islands had migrated westward beyond the Hawaiian volcanic area as, otherwise, representation of the progenitoral forms would be expected in these islands. Because of the former sustained nature of gene flow this hypothesis invokes vicariance rather than "founder effect" as an explanation for Hawaiian endemism.

The topology of the *Priacanthus hamrur* subgroup clade (Fig. 26), and distribution of component taxa (Fig. 20), suggest fractioning of an ancestral taxon having a broad Tethyan distribution from the Indo-West Pacific region, through the Atlantic, into the eastern Pacific. Hocutt (1987) and Springer (in press)<sup>3</sup> have hypothesized that tectonic activities of the Indian Plate have been responsible for vicariant events in the Indian Ocean resulting in isolation of fauna of the western Indian Ocean region from the east Indian-western Pacific. Springer<sup>3</sup> (in press) hypothesized that the suturing of India to Asia at about the beginning of the

<sup>3</sup> Springer, V. G. In press. The Indo-Pacific blennioid genus *Ecsenius*. Smithsonian Contributions to Zoology.

Eocene served as such an isolating mechanism. In the middle Tertiary India probably projected much further southward through equatorial waters prior to subduction of much of the plate beneath Asia. Thus an additional hypothesis is that global cooling and compression of the tropics during the Oligocene (Miller et al., 1985) served to isolate tropical faunas on either side of this prominence. Such an event may be responsible for the initial fractioning of the *P. hamrur* subgroup progenitor with ancestral *hamrur* isolated to the east in the Indian-western Pacific region and *arenatus* + *meeki* + *prolixus* to the west. The sequence of succeeding speciation events is not resolved (Fig. 26) but the closure of the Tethys Seaway in the Mediterranean region during the early Miocene (Hallam, 1981) is implicated in the isolation of *prolixus* in the western Indian Ocean from *arenatus* or *arenatus* + *meeki* (and probable undescribed form from Galapagos region) in the Atlantic-eastern Pacific. Tectonic history would predict a most recent vicariance between Atlantic (*arenatus*) and eastern Pacific populations during the emergence of the Panamanian isthmus in the Pliocene (Jones and Hasson, 1985). This event may be represented in the eastern Pacific by a north Nasca Plate relictual species (undescribed) in the Galapagos plus *meeki* of the Hawaiian Islands. Alternately, the trans-East Pacific Rise event resulting in isolation of the Hawaiian fauna discussed above may have occurred well previous to the Panamanian emergence. The overall scenario is in general agreement with the cladogram of area relationships presented by Hocutt (1987, Fig. 10). Returning to the Indian Ocean, after India had subducted northward sufficiently to lessen its effect as a barrier to tropical marine organisms, *P. hamrur* may have dispersed westward to occupy the western Indian Ocean. *Priacanthus prolixus* may remain as a north-west Indian Ocean (Arabian Sea area) endemic but, based on one specimen possibly from China (see "Distribution" of that species), may have dispersed into the Indo-West Pacific.

Assuming that the apparent absence of a representative of the *P. blochii* subgroup from the mid Pacific Plate region other than the Hawaiian Islands is not a collecting artifact, then at least one ad hoc regional extinction and/or dispersal event must be forthcoming in a hypothesis of the subgroup's biogeographic history. If the subgroup's progenitor had a broad Tethyan distribution and history similar to that hypothesized for the *P. hamrur* subgroup progenitor, then extinction from the entire Atlantic must be reckoned. If, based on present distribution of member species (Figs. 19, 24), a broad Indo-Pacific ancestral distribution is hypothesized, then extinction from, or dispersal across, the Pacific Plate region between Samoa and Easter Island must contribute to explanations of the subgroup's history. The fact that the subgroup is now represented in the eastern Pacific (by *P. alalaua*) but not the Atlantic would favor theories of an Indo-Pacific ancestral distribution and post evolutionary dispersal of *alalaua* to the eastern Pacific from the Hawaiian Islands after the emergence of the Panamanian barrier in the Pliocene.

Sorbini (1983) hypothesized a possible Eocene or older circumtropical distribution for the progenitor of the genus *Pristigenys* based on distribution of fossils and only two of the Recent species. He cited a vicariant mode of speciation without proposing any evolutionary sequence. The topology of the *Pristigenys* clade presented herein (Fig. 26), and the distributions of member taxa (Fig. 11), are partially congruent with those of the *Priacanthus hamrur* subgroup clade with similarly unresolved relationships among taxa occurring in the western Indian Ocean (*niphonia*), Atlantic (*alta*) and eastern Pacific (*serrula*). Tectonic history would predict that speciation events in *Pristigenys* may parallel those in the *P. hamrur* subgroup except that the group failed to be involved or succeed in any trans East

Pacific Rise events (e.g., absence from Hawaiian Is.). It is also necessary to additionally hypothesize extinction of the genus from the eastern Atlantic region.

Finally, the correlation of tectonic plate boundaries with the distributions of many marine fish species expounded on by Springer (1982), and the attendant evolutionary implications, are strongly borne out by distributional patterns in priacanthids. At least 10 of the 18 species appear to have their distributions highly correlated with tectonic plate boundaries, aside from limiting climo-ecological conditions.

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